View metadata, citation and similar papers at core.ac.uk
brought to you by CORE
provided by University of Birmingham Research Archive, E-papers Repository

Author's Manuscript
© David A. Booth, University of Birmingham, UK, October 2013

Chapter in *Nutrition and Chemosensation*, edited by Alan R. Hirsch (Taylor & Francis)

Chemosensory Influences on Eating and Drinking, and Their Cognitive Mediation

David A. Booth
Food Quality Research Group, School of Psychology, College of Life and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, U.K.

Short title Ingestive Chemosensory Cognition

Contents *Page of this MS*

Introduction

The only way that the chemical senses can affect nutrition is by influencing selection among amounts of foods and drinks to ingest. Fundamental to the science of nutrition, therefore, is a correct theoretical understanding of the mechanisms by which tasted and smelled molecules affect the choice of each mouthful, and hence also the number of mouthfuls consumed of each material available on a particular occasion.

Nutritional and other states of the body can also influence choices of what to put in the mouth and swallow. So can the external environment, both physical and socioeconomic. In the human case, social influences can dominate established habits, for example through verbal and numerical signals of information such as the source of the flavouring in a manufactured food, a serving's content of nutrients, and how much of the product people usually eat at one time (Booth, 2008). Nevertheless, all the physiological and social factors in selective eating and drinking have to operate though taste, smell, touch, sight and other senses, because some sensory information is essential to identifying a food or a drink at the point of choice.

In addition, generalist feeders such as humans, dogs and rats have to learn this sensory recognition of a food, and also any contextual factors which influence that food's selection (Booth, 1972b, 1985, 2013; Booth & Freeman, 1993). Therefore a scientific understanding of ingestive behaviour cannot be built merely on measurements of the intake of a food or the verbally expressed strength of disposition to eat it, such as scores for preference or ratings of appetite. It is equally necessary to measure the major influences on each act of ingesting a food or on the rated liking for that item in those circumstances. Only then is it possible to work out how those influences interact to produce that physical or symbolic response to an item – that is, how the chemosensory factors in the behaviour are cognitively mediated.

Basic Theory of Ingestive Behaviour

Neglect of the above considerations has allowed the continuation of a traditional conception of the controls of intake which is erroneous in each of its basic tenets. The size of a meal is not determined by competition between a fixed palatability of each ingestate and a sequence of invariant postingestional satiety signals. After a material has been consumed for the very first time or two, the innate gustatory reflexes to stimulation by sugars, acids, sodium salts, and alkaloids etc., cease to play any role in that material's acceptance or rejection, or the rate of licking the fluid or of biting and chewing the solid. The reflexes are superseded by direct controls of mouthful selection by learnt reactions to many combined attributes, such as salty and sour tastes, a yellow-brown colour, crisp texture, and peer approval. Once a dietary pattern has become familiar, chemical sensing of digestion products in the small intestine and of circulating hormones and metabolites in the brain no longer simply excites or inhibits further ingestion of food. The postingestional signals become integrated in the mind with each item's sensed characteristics and social roles into the state of appetite of the moment, including the depth of its sating by previous ingestion (Booth, 1972b, 2013).

For example, a food that was accepted enthusiastically at its first mouthful in a meal becomes uninteresting or even slightly aversive a number of mouthfuls later (Duclaux, Festhauer &

Cabanac, 1973; Rolls, Rolls, Rowe & Sweeney, 1981a). This particular satiety effect within a meal is specific to the food that has just been eaten, not to a specific sensed characteristic in itself. Rather, the senses are needed to recognise the food that is now less attractive. This mechanism of appetite suppression arises from still unidentified factors such as the specific food's role in the meal, the eater's habitual portion size, a growing boredom with that food and/or habituation of the sensorimotor pathways of its ingestion (Booth, 1976; Meillon, Thomas, Havermans *et al*., 2013).

Hence, as illustrated by the first set of data below, there is no such thing as persisting preference for sweetness as such, in human children or adults, or non-human primates, pet dogs or laboratory rats. Rather, each individual member of an omnivorous species most prefers a particular level of sweetness which is different for each food or drink and context of signals from the internal and external environments (Booth 1985, 2013). This chapter reviews the longstanding and recent evidence that ingestion is controlled by those particular learnt combinations of levels of chemosensory and other signals. The decision on an item in context is read out from a standard in memory built during previous occasions, through readily measured but sometimes unconscious mental processes, into acceptance of an option for the next mouthful.

Excitation and Inhibition of Ingestion by Level of Sweetness

Saccharin Preference as the Model of Appetite

Eating a meal accompanied by a drink is a pleasant activity. Nevertheless, the ingestion itself is often routine and subsumed under other thoughts and/or interactions with other people. When attention is paid to a mouthful, its flavours and textures may be recognised and enjoyed. The expected sensory characteristics may help to motivate selection of an item from the shelf or menu, choice from a buffet or the next forkful from the plate. Unless someone has become very disturbed, for example about the shape of the body, ingestion in itself is not emotional, although the meaning of the occasion or the involvement with a companion may be intensely affecting. Seldom if ever does the sensing of a food or drink generate a physical thrill.

Despite this highly differentiated character of human motivation to eat and drink, animal laboratory research was dominated at one time by the idea that the ingestion of food was completely unselective -- merely a general excitement in anticipation of the scheduled return of food after it had been withheld for a day (Campbell & Sheffield, 1953; Sheffield & Campbell, 1954). Ingestion as a side effect of non-specific arousal was such a deep conviction that it was suggested that learning to avoid dangerous materials was sufficient to explain appetite for nutritious food (Garcia, Hankins & Rusiniak, 1974).

There are indeed very few materials that laboratory rats can be reliably induced to ingest without food deprivation. Even the single complete food on which they are brought up and maintained is eaten in very variable small amounts unless it has been withheld for several hours (Le Magnen & Tallon, 1966). Rats will drink strong solutions of salt when they are in sodium deficit but not otherwise. Only a very sweet solution of saccharin is consumed reliably on first access by an unfasted rat. Hence the volume consumed of a novel saccharin solution was and still is used to measure the conditioning of aversion by association with poisoning or unfamiliar drug effects

(Garcia, Kimeldorf & Koelling, 1955; Massei & Cowan, 2002; Verendeev & Riley, 2012). Saccharin has been mixed with sour or bitter agents in order to suppress its intake sufficiently for nutrient-conditioned preferences to be seen (Pain & Booth 1968; Booth & Davis, 1973).

The distinctive taste shared by saccharin, sucrose and glucose was once regarded as the key to scientific theory of food and water intake, its neuroscience and its societal roles (Pfaffmann, 1960, 1964; Pfaffmann, Norgren & Grill, 1977). The blowfly's consumption of sugar provided an impressively simple model (Dethier, 1962). When its crop is empty, the fly extends its proboscis to secrete fluid onto a lump of sugar and sucks up the solution until the crop is sufficiently distended; then the meal stops.

A solution of saccharin or sugar was treated as the model food and drink for generalist feeders as well. This was despite the fact that major foods (for wild or laboratory rats or for people) do not taste sweet at all. The model of responses to a single taste cannot address the fact that all foods and drinks have other sensed characteristics such as shape, colour, opacity, odour, other tastes and great variety of textures to touch by the fingers, the eating utensil and the mouth. Yet when laboratory research began on effects of physiological manipulations on sensory factors in human appetite for food, the test material was purely saccharin or glucose dissolved in water (e.g., Blundell & Hill, 1986; Cabanac & Duclaux, 1970a,b; Cabanac, Minaire & Adair, 1968; Thompson & Campbell, 1977; Thompson, Moskowitz & Campbell, 1976). Unflavoured sugar water is not liked even by children, unless they were given it as a baby (Beauchamp & Moran, 1982). In order for there to be ingestive appetite, a learnt sensory context for the sweetness is needed.

Ingestive Responses to Sweet Solutions

What then does a sweet taste do to ingestion? We and other omnivores are indeed born with a reflexive reaction, "the sweeter the better" (Tatzer, Schubert, Timischl & Simbruner, 1985). Sweetness in itself speeds and shapes suckling in babies (Crook & Lipsitt, 1976). Sweetness gets young children to consume new foods and drinks. Plainly, though, nobody could ever have lived on sugar alone, or on ripe fruit or honey.

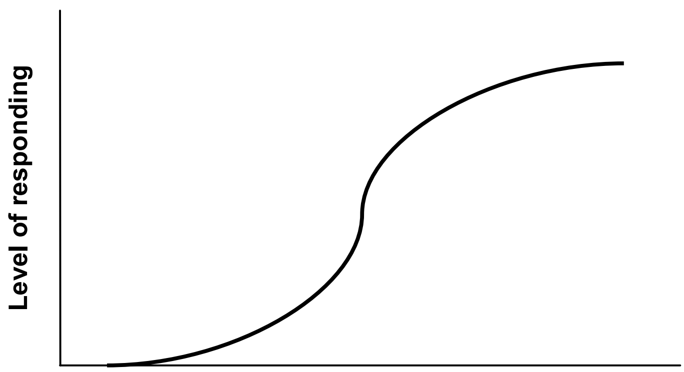
The story becomes more complex if the tested sweet taste comes from glucose (the sugar in mammalian blood) or other sugars (mono- or disaccharides). When solutions are presented one at a time, cumulative intake increases with concentration only to a point: considerably less is ingested of a strong solution of sugar than of a weak solution. This effect is readily explained by an appetite-suppressing effect that develops shortly after ingestion of stronger solutions of sugar has started (McCleary, 1953). This postingestional effect has often been assumed to be metabolic or caloric (e.g., Cabanac & Duclaux, 1970a; Jacobs, 1958, 1962; Jacobs & Sharma, 1969). Nevertheless there is clear evidence that the inhibition from concentrated sugars is osmotic (Shuford, 1959; Smith, 1966; Smith & Duffy, 1957).

Hence, to understand the effect of sweet taste on ingestion, we need to use a molecule that has no other effect than sweet taste, or at least to present a sweet sugar for such a short time that the ingestive behaviour is not influenced by after-effects. Brief tests of rates of licking of glucose solution in rats showed a clear increase in rate with concentration (Davis, 1973). A laboratory rat is provided water all its life through a spout from an inverted bottle. Hence it drinks by wipes of the tongue across the opening of the spout that draw water out into the mouth. These licks become as rapid as possible, with rests every second or so. The greater rate of licking averaged over a minute or so induced by a stronger sweet taste comes from a reduction of the time between the bursts of licking at a fast fixed rate (Davis, 1973).

This facilitatory effect of sweet taste on ingestion increases through all the tested levels, if they are presented briefly one after the other in sequences randomised across rats: the sweeter the stimulus, the stronger the response. That is, the graph of response vigour on stimulus intensity is monotonic (unpeaked). The function is unlikely to be linear, however. It might follow a curve similar to that constructed by Beidler (1954) for responses to tastes in general. This allows for proportionately weaker responses to undetectably low levels and to high levels approaching saturation of the taste receptor. (A similar receptor binding function fits data for odour as well: Chastrette, Thomas-Danguin & Rallert, 1998.)

Such monotonicity is the defining characteristic of an unlearned reflex mechanism. The stronger the stimulus, the more vigorous is the response (Figure 1).

Figure 1. Dependence of the vigour of responding on the intensity of stimulation in a reflex mechanism. The monotonic shape of this output/input function is not mathematically determinate but the vigour of the response rises continuously with the strength of stimulation, from detection of the stimulus at a low level to the approach to saturation of the receptors at high levels.



Reflex Ingestive Movements to Sweet Taste

The newly born infants of omnivorous and frugivorous mammalian species show a fixed action pattern in response to the taste of sugar (Steiner, 1977; Steiner, Glaser, Hawilo & Berridge, 2001). These movements centre on configurations of the tongue that facilitate the transfer of milk to the throat from the breast. The tongue moves forward as far as necessary to squeeze the nipple against the upper gum, expressing milk as the tongue is drawn back into the mouth. In the absence of a nipple, this movement can be visible as a central protrusion of the tongue. The tongue also rolls into a U shape that helps to confine the milk to a flow directly into the pharynx (Iwayama & Eishima, 1997). This curling of the tongue may also be visible if the lips are parted.

These ingestive movements can be observed when a sweet fluid is infused into the mouth of a rat (Grill & Norgren, 1978). Furthermore, if the subcortical regions of the brain critical to ingestion are disrupted pharmacologically, the infusate is not swallowed but dribbles out of the mouth (Berridge, Venier & Robinson, 1989). This is consistent with other evidence that the elicitation of these movements by a sweet taste can be mediated by the brainstem alone. Nevertheless the sweet taste also acts on a part of the diencephalic region activated by ordinary food (Pecina & Berridge, 2005). Hence the sweet taste elicits innate ingestive movements via a subset of the general mechanisms of eating and drinking.

Sensory Motivation without Pleasure or Reward

These reflexive movements of rats and human neonates in response to sweet fluid have been interpreted as a sign of pleasure (Berridge & Grill, 1983; Steiner *et al*., 2001), not just as sensory facilitation of suckling. That separation of hedonic experience from the propensity to ingest was then extended to human adults on the basis of their scores for “liking” or “pleasantness.” Yet sensual pleasure cannot be separated from pleasant eating or drinking merely by differently worded ratings (Booth, 1990, 1991, 2009b; Booth, Mather & Fuller, 1982; see the later section of this chapter on the vocabulary of preferences). Distinguishing a pleasurable emotion from the usual pleasant motivation in adults would depend on the unlearnt ingestive movement reflex to sweetness breaking through a lifetime built norm for a food’s particular levels of sweetness and other sensed characteristics (Booth, 1991).

That dissociation between the reflex and normal learnt performance has recently been achieved, by testing verbal responses to the appropriate combinations of stimuli involving different levels of sweet taste (Booth, Higgs, Schneider & Klinkenberg, 2010a). Signs of the subjective experience of sensual pleasure were indeed seen at a level of sweetness far in excess of that tolerated in the familiar juice in which it was incorporated. Whether a newborn baby or an adult rat is capable of generating such an elaborate private world may be doubted. Adults are built to treat infants sympathetically, regardless of what is actually going on in the very young minds.

Learnt Preferences for Levels of Sweetness

Evidence against all preferences for sweetness being reflexively monotonic was first clearly seen in rats given a continuous choice between solutions of 10 g and 35 g of glucose in 100 ml: the rats started by drinking more each day from the sweeter solution but soon switched to the less sweet solution, and stuck with it (Jacobs, 1958). That remarkable observation was readily replicated (Experiment 1 in Booth, Lovett & McSherry, 1972; this chapter's Figure 2, left-most group). The unlearnt reflexive increase in preference with concentration of saccharin or sucrose (Figure 1) was also seen in initial choices in all subsequent experiments on other pairs of solutions: each group of rats started by drinking more of the sweeter of the two solutions (Figure 2, upper row of panels).

The replication of the switch from 35% to 10% glucose was followed up by a long series of experiments testing various explanations in terms of a fixed mechanism, such as suppression of sweet palatability by sugar satiety, and a more specific proposal that the acceptance of sweet taste is an innate appetite for calories that is progressively sated by consumption of glucose (Cabanac & Duclaux, 1970a). None of those theories gained support from this reversal of "the sweeter the better" (Figure 1).

Finally the two solutions were re-designed to test for explanations in terms of learning from associations between taste and postingestional consequences. Evidence was found for two new examples of classical conditioning, both starting to occur in the first hours of continuous access to the choice between 10% and 35% glucose (Booth *et al*., 1972).

Conditioned Taste Aversion

One mechanism is the conditioning of sensory aversion by osmotic effects. A 35% solution of glucose is extremely hypertonic. (A mere 5% of glucose generates the same osmotic pressure as body fluids). Hence, even if the solution is somewhat diluted by saliva and digestive juices, it is still strong enough to draw water out of any cells it touches. This creates rasping at innervated tissues of the throat, retention of ingested and digestive fluids in the stretch-sensitive stomach, and osmotic expansion of the volume in the duodenal lumen. Disaccharides such as sucrose and maltose are digested to the monosaccharides glucose and fructose inside the wall of the duodenum, doubling the osmotic pressure there from the sugars in the lumen. These postgastric osmotic signals are detected by sensory endings of the vagus nerve in the walls of the duodenum and the portal vein (Hunt & Pathak, 1960; Hunt & Stubbs, 1975; Kelly, 1980; Mei & Garnier, 1986).

The adverse effects of free sugars (Booth, 1979; Booth, O'Leary, Li & Higgs, 2011c) classically condition an aversion to their sweet taste in the mouth, and/or they may reinforce avoidance of the solution that provides that sweet stimulus which is discriminative of the upcoming osmotic punishment. This learnt sensory rejection may be independent of context such as food deprivation or recent feeding, as the suppressant effect of poisoning on saccharin intake can be (Garcia & Koelling, 1966).

Conditioned Taste Preference

The other mechanism involved in the switch from 35% to 10% glucose is postingestional conditioning of sensory preference. The wall of the duodenum has other receptors on nerve endings of the afferent vagus that are chemically specific to glucose (Mei, 1985). The same structures as gustatory receptors in the mouth have recently been found in the intestinal wall, although these receptors function in local regulation of glucose absorption (Mace, Lister, Morgan *et al.*, 2009). Glucose also stimulates chemospecific and metabolomic sensitivities in the brain and in other tissues it reaches after absorption from the small intestine into the circulation (Levin, Dunn-Meynell & Routh, 1999). Stimulation from glucose infused directly into the stomach strongly reinforces preference for any flavour that accompanies or shortly precedes it through the mouth (Sclafani, 1995; Sclafani & Nissenbaum, 1988). Hence the tastes of both 10% and 35% glucose become even more preferred than before learning. However, the punishment by the osmotic effects of 35% glucose is stronger than the reinforcement by its glucose-specific effects and so a net aversion or avoidance of the stronger solution is seen in the relative intakes (Figure 2, bottom left-hand choice).

The design that revealed glucose-conditioned preferences through avoiding immediate osmotic effects by use of isotonic or hypotonic solutions, e.g. no more than 5% glucose or 10% sucrose or maltose, or of the soluble starch product, maltodextrin, in which all the glucose molecules are bound to each other in short chains. A 10%, 35% or even 50% solution of maltodextrin is hypotonic (in a version of that food product which contained only about 3% free glucose and 5% maltose). A stronger conditioned preference was seen for whichever strength of sweet taste was associated with the high concentration of maltodextrin (Experiments 12-14 in Booth *et al.*, 1972; the key data are re-drawn here in Figure 2, right-hand three choices). When the stronger sweet taste was given to the more concentrated carbohydrate, the learnt slope was steeper than the slope of the initial innate preference for the sweeter solution (data not shown here, cp. Figure 1).

Qualitatively stronger evidence for glucose-conditioned sweet taste preference was provided by greater intake of the solution with the less sweet taste after pairing with the effects of more concentrated maltodextrin, reversing the initial innate slope (Figure 2, right-hand three choices, lower panel). The same reversal was produced even by the mildly hypertonic 10% glucose, alongside 3% glucose made to taste sweeter with saccharin (Experiment 12 in Booth *et al.*, 1972).

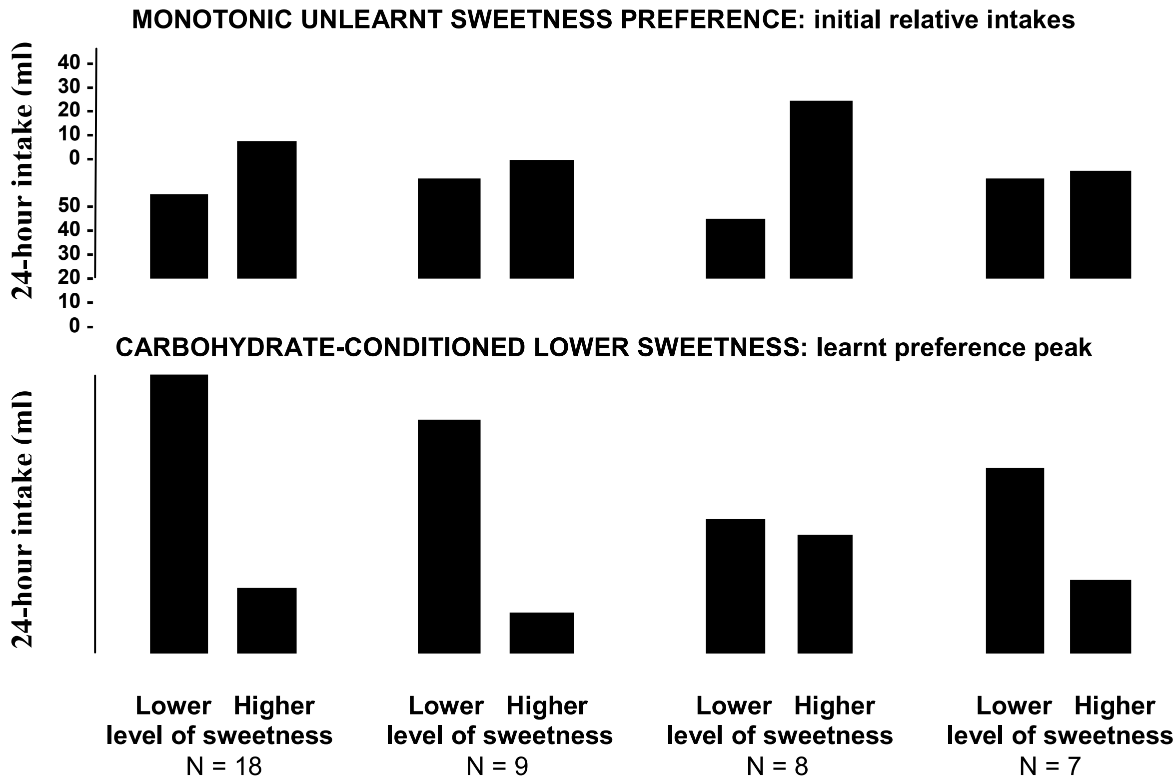
The Learnt Peak of Preference for Level of Sweetener

Preferred Strengths of Sweet Taste

The most important aspect of those findings for the whole field of the chemical senses and nutrition is that the learnt preferences (and aversions) are not for a taste as such. The acquired acceptance is not for a sweet compound regardless of its concentration. The learnt sensory motivation of ingestion is from the particular level of the sweet taste that has been reinforced by some biologically or socially significant event or has become familiar within a context of ingestion. Every detail of the rest of this chapter follows from that single general fact.

Both the conditioned stimuli in these experiments were sweet (Figure 2). The learnt difference in preference, whether in the innate or reverse direction, is between two levels of sweet taste presented side by side. Therefore the learning in each case must be for a particular range or level of sweet taste, not for the sweet taste in general.

Figure 2. Dependence of the vigour of responding on the intensity of stimulation in a learnt acceptance response to a sensory stimulus, contrasted with the initially unlearnt reflex. The response was group mean 24-hour intake volume of each of two simultaneously presented solutions having different levels of sweetness from saccharin and mono-, di- and oligo-saccharides. Greater intake (preference) was reinforced by the postingestional action of carbohydrate content (even at low concentrations). Less intake (aversion) was reinforced by osmotic effects at high concentrations of the monosaccharides glucose and fructose and the disaccharides sucrose and maltose. The initial gradient of preference for stronger glucose was already somewhat reduced by some learning within the first 24 hours to prefer the lower concentration. (Data from Figures 1, 12, 13 and 14 in Booth, Lovett & McSherry, 1972)



The Most Preferred Strength

The level of sweet taste that is ingested in greater amount after learning (lower panel in Figure 2) is likely to be the most preferred level if different levels were tested in short-term tests of relative acceptance. That is, intake would go down at lower levels than the conditioned level, as well as going down at higher levels. A decrease of preference with less of a sweet taste occurs with the unlearnt reflex but this decrease on the lower side as well as the higher side of the learnt level is a characteristic of learnt stimuli of all sorts, usually lacking a reflex.

The above implies another difference between unlearnt and learnt preferences. The unlearnt reflex has smaller responses at lower levels from the highest to the lowest. In contrast, a learnt decline in responses with weaker stimuli starts below whatever level has been conditioned.

This principle of maximum response at the learnt level of a stimulus was established in the early years of research into learning processes. The learnt response became weaker as the strengths of test stimulus were made greater or smaller (Hovland, 1937; Hull, 1947). The learning was not general to all levels of the stimulus. Indeed, the generalisation became weaker and weaker the further the tested level was from the trained level, either up or down. Another way of describing this gradient of decreased generalisation is the detection of increasing dissimilarity between trained and tested stimulus levels (Shepard, 1958).

Hence measuring only the strength of a preference tells us nothing about what is going on. The variation of degree of preference with amount of stimulation needs to be measured. Then we know something about what the preference is for. Indeed, if we collect adequate data, we can estimate the most preferred level of the stimulus, i.e. which amount was trained (without ever observing the learning process), and even how sensitive the preference response is to differences in level of the stimulus.

Such characteristics of learnt acceptance of stimuli in foods and drinks are a foundation for a complete science of the sensory, somatic and social controls of ingestive behaviour. The rest of this chapter provides examples across the major chemosensory influences on selection of mouthfuls.

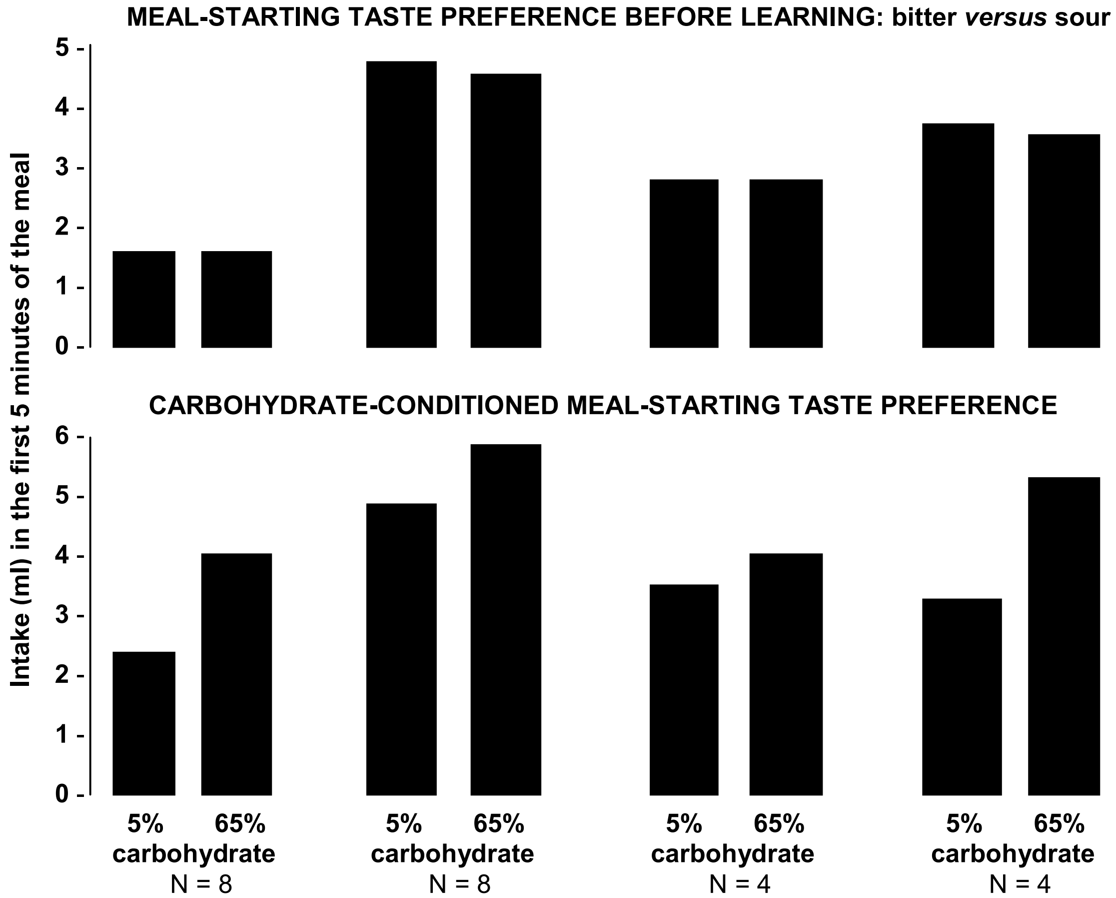
Somatic Contexts of Sweet Preference

When a single sweet solution is presented to a rat which is strong enough in saccharin (0.2%) to elicit reflexive ingestion, the inclusion of a little glucose (3% - so little that it can barely be tasted on its own) conditions preference for the sweet taste so powerfully that the rat rapidly comes to drink half its body weight of the solution each day (Valenstein, Cox & Kakolewski, 1967). This extreme fluid intake does not occur with higher concentrations of glucose because of the immediate appetite-suppressant effects of their osmotic strength (Shuford, 1959; Smith, 1966), ahead of its associative conditioning of aversion to the taste. However when the free glucose is replaced by its bound form in a soluble breakdown product of starch (maltodextrin), there are no longer immediate osmotic effects in the mouth and throat; osmotic effects can only arise after digestion frees the glucose. Then the conditioned preference for the specific taste given to the solution induces increasingly large intake during a limited period of access to the single solution (Booth & Davis, 1973; Figure 3).

The specificity to the preference-conditioned taste was shown by providing a brief choice at the start of the daily test period between tastes previously paired with different concentrations of carbohydrate. In the 5-minute choice period, more was drunk of the taste that had previously been paired with a high concentration of maltodextrin than of the taste paired with a low concentration of sugar and starch (Figure 3, lower panel). This showed that the larger amount of carbohydrate associatively conditioned the greater sensory preference.

Nevertheless, maltodextrin is eventually digested to glucose. First maltose is released by amylases in the lumen of the duodenum. That disaccharide is then broken down to glucose on the inner side of the wall of the duodenum. Hence the 65% maltodextrin could produce a high

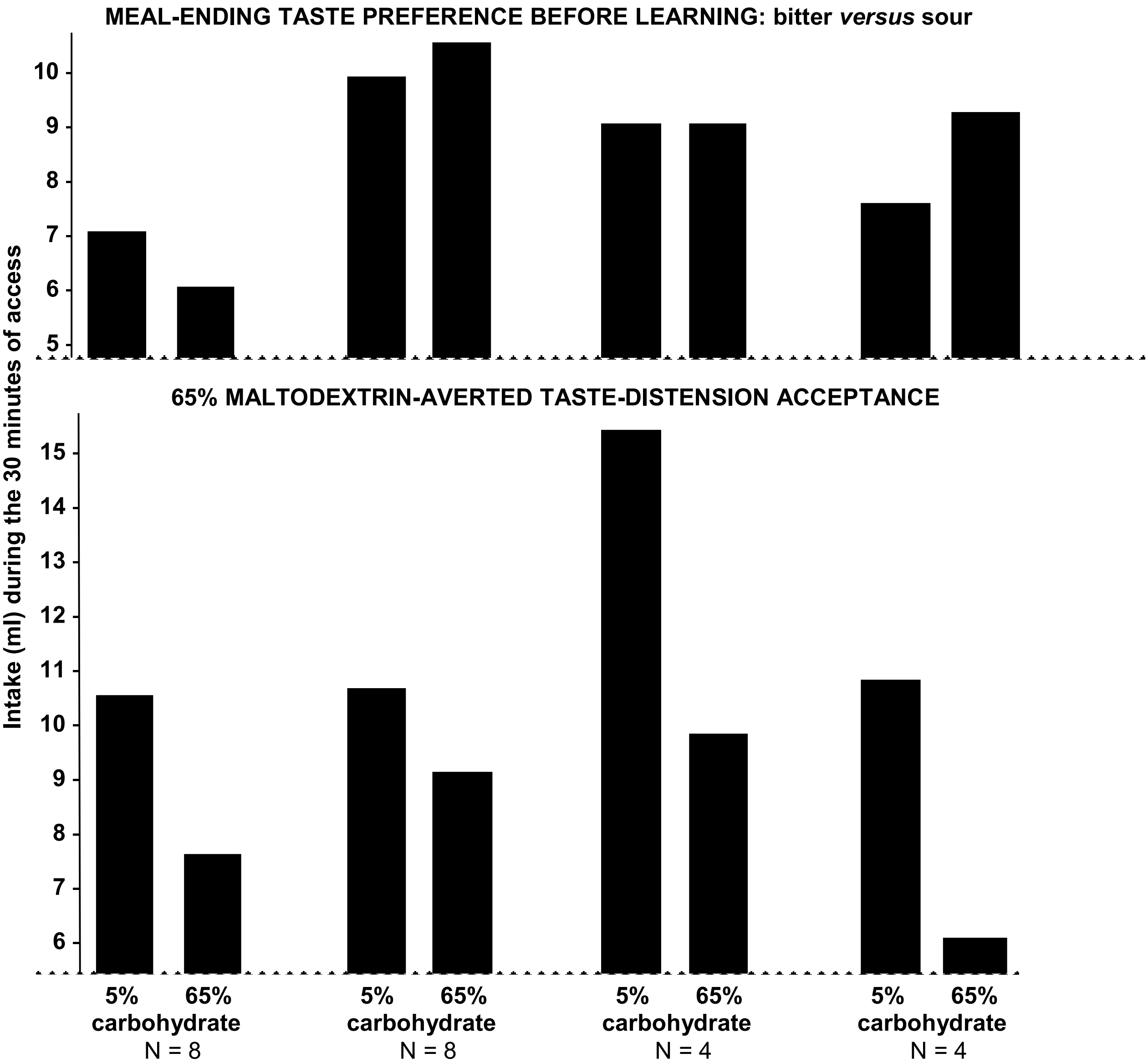
Figure 3. Meal-starting taste-specific intakes (ml in the first 5 minutes of 30-min access) at the start and end of pairing one taste with 65% carbohydrate (low-glucose maltodextrin, with no immediate osmotic effect) in 12 30-minute test sessions (meals) and the other taste with 5% carbohydrate (3% starch gel, 2% glucose) in another 12 sessions (although the final difference began to emerge by the second to fourth session (from Booth & Davis, 1973). The two solution had similarly sweet tastes from glucose supplemented by maltose or saccharin, and were differentiated by either citric acid at 200 mg per 100 ml or quinine sulphate at 0.5 mg per 100 ml, balanced across rats. Rats generally drank very little of each taste in the first 5 minutes of the initial sessions and so the starting intakes (upper panel) are taken from the average of the first pair of sessions with substantial intake. Intakes in the final sessions (lower panel) showed that 65% maltodextrin conditioned a stronger preference to the initially aversive taste mixture than did the 5% carbohydrate.



concentration of glucose at osmoreceptors as well as glucoreceptors in the wall of the duodenum and the portal vein from the small intestine to the liver. If that occurred while a flavour was being consumed, the result could be a conditioned aversion.

In these experiments, however, the same flavour is being presented throughout the meal. The net effect of glucose-conditioned preference and osmotically conditioned aversion remains a preference, at least at the start of the meal (Figure 4). Therefore some other stimulus is needed to predict the transient osmotic signals from digestion of maltodextrin. The most reliable contrast

Figure 4. Taste-satiety configured meal volumes (30-minute intakes in ml) before and after learning, showing a switch from larger meals on the thick and perhaps sweeter 65% maltodextrin to smaller meals (with taste the only difference, both tested in 35% carbohydrate), while the preference for 65%-paired taste persist in choice tests between two bottles simultaneously (Booth & Davis, 1972: their Figures 1 & 3). The switch is explicable only by the taste being configured with satiety signals, such as a substantial volume in the stomach or a decline in ghrelin secretion, and that taste-satiety combination becoming averted by the delayed osmotic signal after duodenal digestion of maltodextrin (the conditioned satiety of Booth, 1972b, 1985, 2009a, 2013). These meal sizes come from the same experiments as the meal-start data in Figure 3 (comparable with the design in Booth, 1972a).



with the start of the meal could be the amount in the stomach during release of maltose in the lumen and glucose in the wall of the duodenum. Hence the relatively mild punishing effect of transient high osmotic strength of glucose from concentrated maltodextrin could counter much of the preference conditioned by glucose if it were tied to the combination of that level of sweet taste and a stimulus specific to the later part of a meal, such as a neural or hormonal signal from a relatively full stomach (Booth, 1972b; Booth & Davis, 1973; Booth, Lee & McAleavey, 1976).

In other words, this osmotically reduced facilitation (or actual inhibition) of acceptance is a learnt response to a level of gastric distension as well as to a level of sweetness (Booth, 1985, 2009a, 2013). Therefore, for this interoceptive stimulus also, there should be a decline in learnt response on either side of the conditioned level of distension. Ingestion itself may well remain inhibited, nevertheless, even though distension has increased beyond the conditioned level and so its satiating effect is reduced. The overall satiation is then coming from postgastric signals as well (Kissileff, Booth, Thornton *et al*., 2008, and in preparation).

Evidence that Human Sensory Preferences are Learnt

The above analysis implies its inverse. If a preference response peaks at a particular level of a stimulus, this is evidence that the preference has somehow been learned. That conclusion follows without any observations of the learning process. Such research into the human acquisition of preferences for novel materials is needed in order to elucidate factors which support or disrupt the learning process, but not to establish that the preference has been learnt.

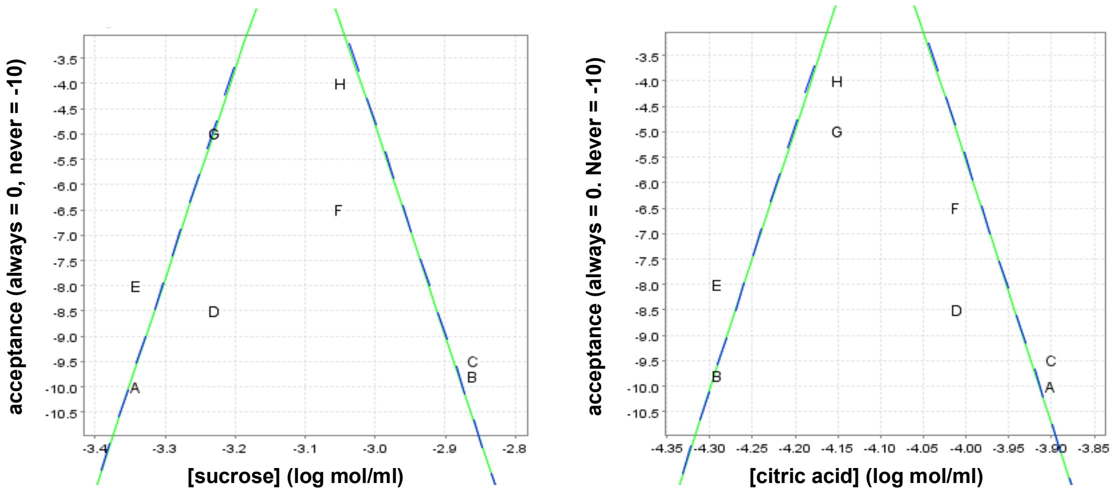
Indeed, demonstrating the learning of food preferences is a thankless task in adults brought up on a varied diet and flexible eating practices. The experimenter’s manipulations have to build on a lifetime of learning. A successful experiment is likely to have exploited a higher order mechanism for ready changing of preferences, rather than demonstrating the existence of a basic mechanism, such as habituation or reinforcement (cp. Kerkhof, Vansteenwegen, Baeyens & Hermans, 2009). Similarly, failures to condition preference can be attributed to designs that are unrealistic to routine choices (cf. Durlach, Elliman & Rogers, 2002).

Nevertheless, adequate measurement of the sensory basis of an existing preference can reveal something of the original learning, whether by familiarisation, conditioning, reward or attitude transfer. The level of the stimulus at maximum preference points to the material and situation that the child or adult has learnt about. Widely available versions of a food or drink may differ in level of sweetness or some other sensory factor, or in timing within the meal or other somatic or social factors. The most preferred sweetness and the appropriate stage in the meal are both liable to be the result of the use of the variant of the food that has that sweetness in that position within meals (Conner, Haddon, Pickering & Booth, 1988c).

The Peak of Learnt Facilitation by Any Sensory Factor

In the above experiments in rats (Figures 3 and 4; Booth & Davis, 1973), the two conditioned tastes had a similar level of sweet taste and so that was the location of the peak of the learnt sweet preference. However, citric acid was added to one sweet solution and quinine dissolved in the other, in order to enable the rats to predict the distinction between their consequences. (The higher carbohydrate concentration was paired with the sweet-and-sour taste or the bitter-sweet taste in equal numbers of rats.) The implication is that both the sweet taste and also the sour or bitter taste had each acquired its own peak preference level, as we can see from later human data (Figure 5).

Figure 5. One assessor's degrees of preference for mixtures of sucrose and citric acid in a familiar orange-flavoured still drink, plotted separately for the independently varied levels of sugar and acid. Sequence of presentation was from mixture A first to mixture H last. Ratios of tastant concentration are fitted to a symmetrical peak of preference rated from "always choose" (scored as zero) to "never choose" (-10). Linear fits account for much less of the variance. [Replotting of raw unfolded data in Booth (1994), Figure 5.3]



Mixtures of sweet and sour taste compounds commonly occur in fruits, and in drinks prepared from them. When the levels of sweet taste and sour taste are varied independently of each other in a familiar orange-flavoured drink, it becomes obvious that the learnt personal ideal for sour taste has a peak just as the learnt sweet taste preference does (Figure 5). The same presumably happens for the aroma and colour of a breakfast drink, since an ideal point appears for the strength of a breakfast drink composed of flavouring and colouring as well as sugar and acid (McBride & Booth, 1986).

Therefore the default position has to be that any sensory facilitation of ingestion, including by tastes and smells, must have been acquired by personal experience. Indeed, preferences are likely to be so well learnt that changes in preference will be hard to induce in the laboratory or in life. The idea of acquiring a completely new preference is probably a misconception. In theoretical principle, even just trying a novel food or drink requires a preparatory context or some sampling incidental to existing habits. Once the shift in sensory stimulation has been experienced, its learning might be fast if there is a background to extend; otherwise the learnt preference might be weak and its acquisition slow. Early laboratory evidence of learnt appetitive food stimuli in animals emerged only after prolonged training (Booth & Miller, 1969), unless a single exposure was very intense (Booth & Simson, 1971).

Learnt Likings for Levels of Bitterness

The unlearnt reflex movements to a bitter taste are expulsive, such as gaping in rats and human neonates, and spitting in older children. The expulsive reflex movements are suppressed, however, when the bitter substance is in an already familiar material that has become acceptable. Adults acquire ingestive preferences and appetites for intensely bitter materials, when the level of bitter taste is appropriate to the context of other sensed features, such as aroma, colour and temperature. Strong coffee is a prime example. In some people, the learnt reaction may be a purely sensory preference, extending to the decaffeinated version of the usual brand of coffee. Nevertheless, the drinking of coffee can be the expression of a whole appetite for caffeine, involving expected pharmacological effect and current social context.

Conditioned Appetite for Caffeine

An individual's adenosine neurotransmitter receptors can become adapted to high circulating levels of caffeine. The heavy user of caffeinated drinks may be sensitive to a decline of concentration in the blood when no caffeine has been ingested for several hours. Restoration of caffeine levels by consumption of a distinctively flavoured caffeine-containing material can then condition a preference for that material. This caffeine-conditioned sensory preference is greater when blood levels of caffeine have declined again (Yeomans, Jackson, Lee *et al*., 2000). That is, that material's consumption has become an appetite specific to the combination of the sensory characteristic of the material and a circulating concentration of caffeine below the adapted level.

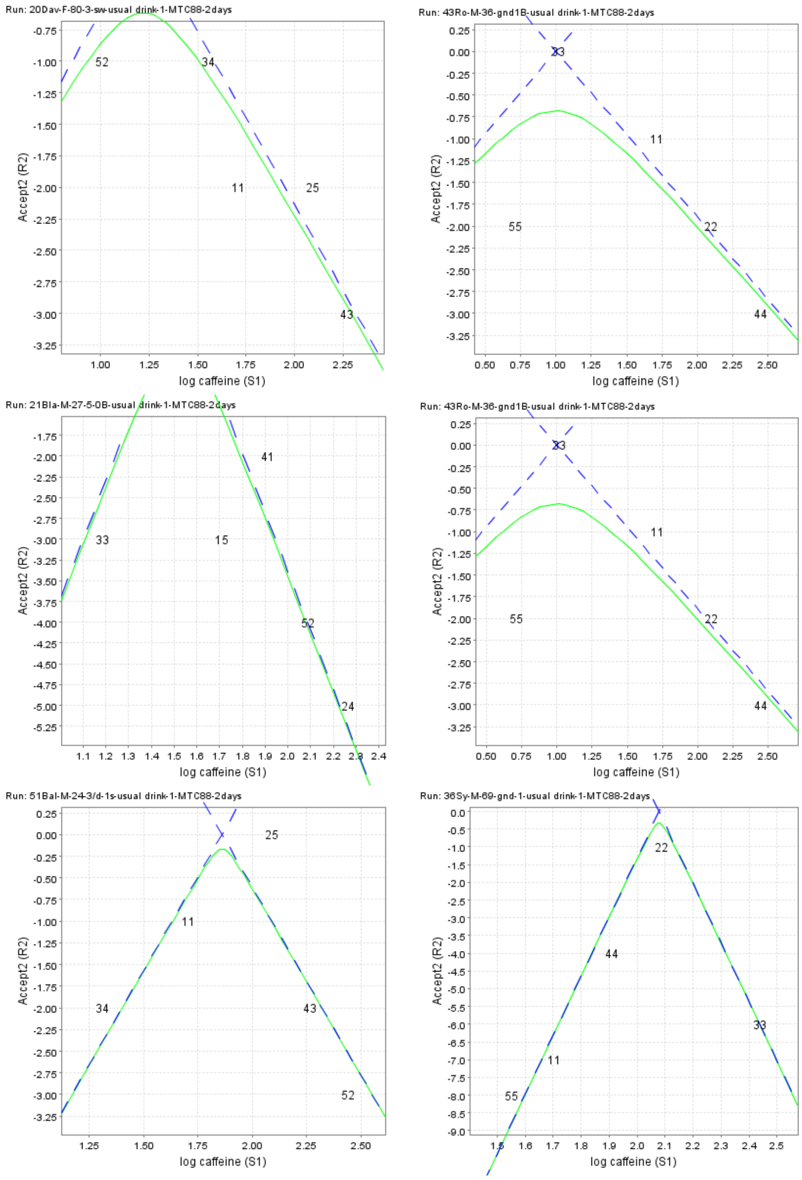
Ideal Point for Bitterness of Caffeine

As with sweet-tasting compounds, the learnt preference or appetite for the bitter taste of coffee (whether or not reinforced by pharmacological effects of caffeine) proves to be an acceptance that peaks at a particular level of the coffee's bitter taste, and not for the bitter taste at any intensity, either higher or lower. This ideal point for bitterness in the personally familiar drink of coffee was demonstrated in an experiment looking for variation with age in taste sensitivity to differences in concentration of caffeine (Booth, Conner & Gibson, 1989; Booth, Sharpe & Conner, 2011d).

The roasting of coffee beans generates many bitter compounds that add to the taste of the caffeine already in the beans. So the level of bitterness can be varied adding different amounts of caffeine to a decaffeinated product. When the test session is spent on mouthfuls of the drinker's usual coffee with widely varying caffeine contents, the gustatory effects of caffeine are disconfounded from its pharmacological effects during or after the session, as well as from any expectations of later effects of ingested caffeine if the assessor believes that different strengths of roast are being compared, rather than different levels of caffeine.

Acceptance of samples of the assessor's usual coffee varied only in caffeine content always peaked somewhere between the lowest and highest levels tested (Figure 6). Hence the preference or appetite for the bitter-tasting drink had been acquired. It was not, for example, a reversal in direction of a monotonic reflex mechanism from expulsive to ingestive.

Figure 6. Preference peak ("always accept" = 0) for caffeine in the individual's usual coffee for two assessors at each quartile of that ideal level of coffee (total N = 52). Upper panels: lower quartile. Middle panels: median. Lower panels: upper quartile. Caffeine concentrations in the $\log_{10}$ mg per cup (150 ml). Calculated by CoPro tool from data collected by Mark Conner for Booth, Conner and Gibson (1989). The group distribution of the personal ranges of ideal point was reported by Booth, Sharpe and Conner (2011c).



Development of Preference for Bitter Foods and Drinks

Individuals' ideal points and differential sensitivities for the taste of caffeine varied widely, with no clear relation to age group or gender (Booth *et al*., 1989). It is important to note that those who had the lowest ideal points or greatest sensitivities were still habitually drinking caffeinated coffee. Furthermore, ideal points were not substantially correlated with sensitivities.

There is indeed no reason to expect adults' likings for coffee to be related to sensitivity in discriminating or detecting bitter tasting compounds, or indeed coffee's strongly sour constituents. There are many ways of preparing a drink of coffee and therefore at least as many routes to growing to like one or more of those versions. Young people may start drinking coffee with sugar or milk, or as a weak infusion, but in some societies there is no standard adult version. Personal exploration or peers' habits may lead to strong infusions with or without sugar and/or milk, mild roasts with a little or a lot of milk, or other variants. Availability may shape a habit of using ground coffee or instant coffee. Good or bad experiences with pharmacological effects of caffeine on the brain or the kidneys and bladder may affect choice of strength of coffee, and hence the preferred taste, as well as the frequency of coffee drinking.

The same diversity of options applies to the bitter tastes of chocolate, grapefruit and cheese. The intensity of taste (and aroma) of a mature cheddar or a blue cheese which tastes very bitter to an individual may lead to great enjoyment of a small piece with butter on a cracker, with a mild cheese being quite unacceptable. The main disruption to normal acquisition of liking for a bitter-tasting food may the initially sampled taste being too strong and not having any of the incentives that others have to try that food again, such as participation with peers or carers.

In short, even though bitter agents are innately rejected more vigorously at higher concentrations, familiarity and reinforcement of some bitter taste in a particular food or drink will create a most preferred level for bitter taste in that item when consumed in its usual context. *A fortiori*, individual difference in inborn reflexes to a taste need bear no general relationships to preferences for foods having that taste,

PROP and Food Preferences

The principle of diversity of developmental pathways applies to any source of stimulation to the taste receptor family for plant poisons. A minority of people inherit a strong sensitivity to the bitterness of a compound commonly known as PROP (Bartoshuk, Duffy & Miller, 1994).
It has been widely assumed that such people must dislike foods that stimulate the same part of the large family of bitter receptors.

In fact, the evidence is far from conclusive that PROP sensitivity always puts people off bitter foods for life. An undergraduate project screened for high sensitivity to PROP by the standard filter paper test and found that such people tended to like medium-strength Cheddar cheese better than those who did not taste the PROP on the paper (Stroud & Booth, 1999). Indeed, a simple cross-sectional relation of PROP sensitivity to aversion to bitter foods far from clear in the literature. The chances that sensitivity to PROP relates systematically to nutritional health through dietary habits are therefore quite remote.

There are undoubtedly genetic influences on human behaviour, as well as environmental factors. Nevertheless, genetic expression interacts strongly with environmental exposure continuously throughout life. Hence, a search for simple associations is highly questionable. Rather than the simplistic model of genetic determinism, it could be more productive to search for genetic vulnerabilities and environmental stressors with a view to specifying the variety of more prevalent interactions among them (cp. Rutter, 2008).

Human Preference for the Taste of Salt

Many non-human omnivores have an innate appetite for sodium chloride (Denton, 1982). That is, when the animal in the wild goes into sodium deficit, it seeks out materials tasting of salt and consumes them. Laboratory rats can learn ways to get salt before ever becoming sodium-deficient (Krieckhaus & Wolf, 1968).

At birth, human infants are relatively insensitive to the taste of salt. Yet within a few months, they are capable of discriminating between levels of salt in human milk and in a supplementary or weaning food such as cereal or mashed potato, and preferring the level of salt they have been exposed to, both abilities measured by how much they eat in a test session (Harris & Booth, 1987; Harris, Thomas & Booth, 1991). These findings have been replicated in a larger group of 6-month-olds, using a contrast with exposure to fruit which is much lower in salt content (Stein, Cowart & Beauchamp, 2012).

By young adulthood at the latest, preferences have developed for the particular levels of the taste of salt in each familiar food, including bread, mashed potatoes and soups of chicken or tomato (Booth, Thompson & Shahedian, 1983; Conner, Booth, Clifton & Griffiths, 1988a; Shepherd, Farleigh & Land, 1984). (These are all prepared foods with culturally conventional levels of salt and there is no possibility that the diverse most preferred levels are innate.) Furthermore, there is a very sharp peak of personal preference when plotted against salt concentration in test food which is close in other characteristics to the individual's usual version, as for the taste of sugar in a familiar food or drink (Figure 4). Adequately refined designs to identify increased preference for salt during sodium deficit, whether innate or learnt, should measure each individual's salt preference function and look for within-subjects rises in ideal points and/or increases in tolerance slope (Conner *et al*., 1988a). Individuals' preference scores by themselves cannot show what is going on, especially in tests on salt solutions out of the context of a familiar food (Cowart & Beauchamp, 1986).

There is some evidence in human adults of temporarily increased intake of familiar higher-sodium foods after depletion of sodium ions by prolonged sweating (Leshem, Saadi, Alem & Hendi, 2008). That also could have been based on earlier learning from eating salty foods while body fluids were depleted. Any permanent enhancement of human salt intake by sodium depletion appears to be limited to the period around birth (Leshem, 2009).

Tastes, Smells, Colours and Textures

The evidence from rats and people therefore supports a generalisation to any sensory factor in an individual preference for a particular item. The mechanisms for acquiring a maximum preference for a specific level of sweetness in each food and drink in the usual context of consumption are activated for any sensed characteristic of the familiar option. Indeed also any somatic or social signal that is familiar or has been reinforced has an ideal point for each context in which that signal occurs.

The chemical senses extend beyond taste and smell. Irritation (mild pain) is also chemospecific (Dessirier, Simons, Iodi Carstens *et al*., 2000). Irritative agents in foods and drinks that are liked at particular levels range from carbonation to ginger, pepper and chilli. The theory is that each substance has a peak-preferred level for each person in each familiar fizzy drink or spicy food. Colour is a key part of flavour as ordinarily experienced and can be regarded as the photochemical sense: the retinal pigments differ in amino acid sequence at their photon-sensitive sites. Consumers' choices cluster around the intensity of hue given to a manufactured product (Conner, Pickering, Birkett, Booth, 1994).

The physical texture (mouthfeel) of a food or drink is also often included in everyday impressions of flavour. For example, the astringent 'taste' of tea is in fact the texture of salivary proteins denatured by the polyphenols in the brew (Breslin, Gilmore, Beauchamp & Green, 1993; Horne, Hayes & Lawless, 2002).

Many other textures depend to a considerable extent on chemical composition, although purely physical factors are sometimes crucial, e.g. the distribution of fat globule sizes in dairy cream (Richardson & Booth, 1993; Richardson, Booth & Stanley, 1993; cp. Booth, 2005). Nevertheless the same principle applies. For example, each regular user of light cream has an ideal level of viscosity, and does not act as though "the thicker the better" (unless they really prefer super-heavy cream in their coffee, or butter in their tea in the Tibetan tradition). Users of cream in whole milk yogurt are also liable to have a most preferred range for the diameters of the fat globules. Similarly, the crispness of lettuce or the crunchiness of a type of cookie has an ideal level of each physical component of the heard or felt characteristic for each user, depending on experience of the particular food (Booth, Earl & Mobini, 2003a; Booth, Mobini, Earl & Wainwright, 2003b,c; Vickers, 1984).

Missing the [Ideal] Point

Group-Averaged Scores for Preference

Failure to attend to the relationship of degree of preference to amounts of chemical stimulation has repeatedly disrupted progress in research into the role of taste or smell in nutrition. The reality needs to be faced that each individual has a most preferred level of a sensory factor in a context of food choice, and a particular sensitivity to deviations from that ideal point. Those are the characteristics of ingestive behaviour that should be profiled across people and foods, as illustrated elsewhere in this chapter. Instead, the raw scores for quantities of pleasantness or ranks of liking have been averaged across groups. Worse, aversion has been confounded with preference by putting unpleasantness or dislike into those scores or rankings of preference using the term ‘pleasant’ or ‘like.’

Yet this poor measurement of degree of preference is not the most serious problem with these research areas. Whatever measure of degree of preference is used, it is the influences on preference that are relevant, not just how much a food is preferred.

Food Preferences and PROP Genetics

Most of the research into genetic variation in the bitter taste of PROP (mentioned above) has been based on average scores for the degree of preference for each named food. Such scores convey no information about the contribution of bitter taste or any other factor to the individual’s present acceptance of that food (by whatever pathways it developed). A simple illustration of the scientific use of preference scores was given above for the taste of caffeine. The ideal points estimated in that experiment were distributed in a pattern reminiscent of that observed in much more complicated measures using the unscientific concept of an absolute threshold. That pattern of most preferred levels is as expected for a division of the population into tasters and non-tasters of PROP, with a subcategory of generic supertasters (Booth, Sharpe & Conner, 2011d).

A realistic approach would start with specifying each individual’s current frequency of use of foods having a substantial bitter taste, with a view to identifying foods eaten by a sufficiently high proportion of the sample to be useful for genetic analysis. Then the influence of a constituent stimulating a broad profile of bitter taste receptors on the liking of each widely eaten food would be measured, using samples that differed only in concentration of that constituent. This sensory contribution to preference for each of several common foods in each person is measured as the mathematically independent values of differential sensitivity (not detection sensitivity) and ideal point (not preference score). These are the two phenotypic characteristics for each food (or a multivariate if highly correlated) that should be used for genetic screening and differentiations between PROP tasters and non-tasters (compare studies such as Chang, Chung, Kim *et al*., 2006; Ditschun & Guinard, 2004; Tepper, Koelliker, Zhao *et al*., 2008).

Food Preferences and Obesity

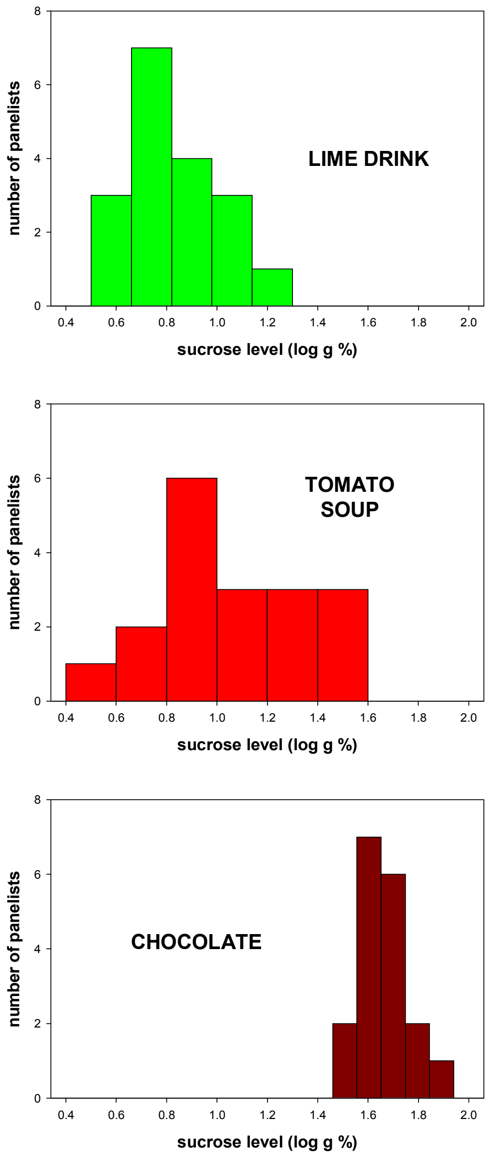
The increasing prevalence of obesity has often been blamed on the attractiveness of sugars and fats. However the leanest people eat attractive foods! So this attack on the commercial suppliers requires evidence that fatter people have stronger likings for the sensed characteristics of sugary and fatty foods.

Sweet taste

Way before claiming that sugar is addictive, we first have to see if widely consumed foods or drinks are more preferred when given the sensed characteristics of extra sugar. As should be clear by now, this is an ill-formulated question, since there is not a one-to-one relation between combinations of sugar with other constituents and degrees of preference.

Whenever one sensory feature, but nothing else, is varied in a familiar food, each person is found to have acquired a most preferred level. This was established first for salt in soup and bread (Booth, Thompson & Shahedian, 1983; Conner *et al*., 1988b; Shepherd, Farleigh & Land, 1984). Then it was shown many times for the sugar content of a variety of foods and drinks (Conner & Booth, 1988; Conner *et al*., 1986, 1988b). Consistent with the ideal point being a product of learning, these personally most preferred levels cluster around the levels in the most popular brands of that food. This applies to sweet taste as much as to any other sensed characteristic (Figure 7).

Figure 7. Distributions of personal ideal points for sugar in an uncarbonated limeade, canned tomato soup and chocolate, in a panel of 18 assessors (data from Conner *et al*., 1988b).



Each participant's preference for the food or drink peaked at a particular level of sucrose, rather than increasing indefinitely. Many people preferred even the relatively sour drink and a soup to contain less than 10% sucrose (1 $\log_{10}$ g/100ml in Figure 7), a rule-of-thumb that has been suggested. Also the mode for ideal point (IP) varied among the three tested materials. In each case, the mode was in the range of the levels available in the market and therefore expected by users of the product. The ranges of sucrose concentration and the widths of the 5-6 bins in Figure 7 may also reflect variability among participants in the most familiar version of the products. Indeed, the pattern of IPs differed between participants who used manufactured sweet foods and drinks, such as chocolate and fruit drinks, and users of fruit and sweet vegetables such as carrots (Conner & Booth, 1988).

Plots of concentration of sweetener (or intensity of sweetness) against the individual's degree of preference (e.g. rated pleasantness) are seldom constructed correctly. The individual's peak preference for sweet taste in the test food is often not measured, nor even allowed for in the presentation of the data. Indeed, for a long time, research into the role of sweet taste in obesity used plain solutions of sugar or saccharin, not universally familiar sweet drinks or foods, and did not anchor the ratings on the usual or most preferred version of each material in a particular use.

An early comparison of obese and lean people that plotted individuals' pleasantness ratings against sugar levels had the essential merit of testing a real food material, namely fruit cordial (Witherley & Pangborn, 1980). Likers of sweetness were expected to show a positive slope (as in Figure 1 above), while sweet haters were thought to give a negative slope, as to a purely aversive taste. The authors despaired at the variability of slopes in both the fatter and leaner groups, from a wobbly flat line to a steep slope that was sometimes positive and sometimes negative in each group. Yet either slope can be created in the same individual by testing levels of sweet taste in a familiar food that are all on one side of that person's ideal sweet intensity for that food. A positive slope shows that the levels in the samples are all below ideal or close to it. Samples solely or mostly above ideal should give a negative slope (e.g. top left panel in Figure 6). Furthermore, if the individual had never consumed the cordial on its own, an ideal sweet taste could not have been acquired and the pleasantness/sucrose function might be flat. If the ratings of pleasantness had been anchored on the most preferred sweetness, it would have been simple to estimate each participant's ideal point and compare the distributions of this most relevant personal characteristic between the two groups.

Even more seriously, the usual practice then, and still to this date, has been to average the preference score for each tested material and plot those mean values against concentrations or intensities of the sensory factor. In statistically more elaborate analyses of grouped data, the profile of preference scores is smoothed by fitting the data to a polynomial regression or by non-metric multidimensional scaling. The result is a conflation of the raw data that has no theoretical basis in the mechanisms of sensory preference. Such neglect of individuals' precise achievements is unnecessary. The group's data are as clearly summarised in histograms of the prevalence of ideal points in each range of sweet taste (cp. Figure 7; contrast the usual umbrella graphs and contour maps drawn from grouped raw scores, for example in Drewnowski *et al.*, 1982, 1985; Drewnowski & Greenwood, 1983).

If fatter people do have higher ideal points for sweet taste, or sweet taste makes stronger contributions to their preferences, that finding by itself does not show that a liking for sweetness causes obesity. Both obesity and ideal points for sweetness come from eating habits. Whether or not a particular habit is fattening is a further question that has yet to be adequately addressed for any common pattern of eating or drinking, including one majoring on sweet materials (Booth, Blair, Lewis & Baek, 2004; Laguna Camacho & Booth, under review).

In the UK, there appeared to be two forms of sugar preference ('sweet tooth'). One had lower maximum sweet preferences, coming from frequent use of fruit. The other had higher ideal points, attributable to frequent use of sweet packet foods (Conner & Booth, 1988). A somewhat similar differentiation was evident more recently in the USA (Wansink, Bascoul & Chen, 2006). However, obesity cannot be caused by the mere existence of greater amounts of sugar in cookies and candy than in apples and carrots: the foods have to be ingested. The question is whether a switch in consumption from sugary foods and drinks to fruit and vegetables reduces daily energy intake, after the amounts consumed of other sources of calories have adapted to the change. The experimental design needed to answer that question within and across localities has yet to be run, several decades after it was formulated.

Fat 'taste'

Preferences for fats in foods have been attributed to the "taste" of fat. However triglycerides do not stimulate gustatory receptors. Fats have aromas derived from their sources: a major factor in the attractiveness of butter and cream is their dairy aroma (a low level of the smell of the cow!). Hydrolysis and oxidation of fats during cooking produces short-chain fatty acids, ketones, aldehydes, etc. Some of these compounds have sour and/or bitter tastes but again mostly an obvious and behaviourally influential aroma.

Liquid or solid fat by itself is not attractive. Even for those who like it as a dressing, it needs the taste and smell inherent in olive oil or added as vinegar. A lot of the attraction to fats in foods arises rather from tactile textures. Dairy cream is an emulsion with a thick and smooth texture. Such sensed physical characteristics such as high viscosity, low stickiness and precise globule size distribution are critical to the authentic creaminess of yogurts (van Aken, 2010; Booth, 2005, Richardson *et al*., 1993). The fat in baked goods such as cookies forms planes along which rock-hard starch-protein matrix and sugar crystals can be pressed apart by the teeth (Booth, Mobini, Earl & Wainwright, 2003b; Vickers, 1984). The vegetable or animal fat in baked products such as cookies and cakes, and fried foods such as potato slices and sticks, creates micro-regions of softness within a matrix of hardened gels of starch and protein, generating various types of crispness, crunchiness and crackling texture.

The fat in ice cream is crucial to retaining dairy, vanilla and fruit aromas, and to breaking up the hard texture of ice crystals. Nevertheless fruit ices without fat are also popular. Hence people might vary in their ideal points for each element in the complex of sensory contributions from the amount of fat in ice cream. There is lots of sugar in both types of ice. Unfortunately, however, data on personally ideal levels of fat and sugar in ice cream have been buried in polynomial regressions through raw preference scores. These profiles (or 'umbrellas' fitted to preference scores for fat and sugar) provide very coarse measures, making group differences hard to replicate and limiting the breakdowns by age-group and gender that are important in relating eating habits to obesity. It would be more productive to look for differences in frequencies of use of foods have divergent fat contents.

In fact, the usual approach of relating food preferences to obesity is ill founded because of lack of evidence which patterns of consuming foods containing sugar and/or fat do indeed fatten the individuals who have those habits. Hence warning labels "Fattening. Keep off" cannot be justified, unlike the message that smoking causes death on cigarette packs. Indeed there remains no firm evidence that sugars are any more fattening than other sources of energy, although the timing of sugar sodas between meals may be a problem (Booth, 1988; Booth *et al*., 2004). Fats are liable to be more fattening than carbohydrates or proteins, calories for calorie, but there is still no measure how much weight is lost from reduction in frequency of eating any particular higher-fat option (French, Jeffery & Murray, 1999; Laguna Camacho & Booth, under review).

The Family Paradox

Generations within a family share substantial backgrounds of both genes and environment. Hence there is reason to think that they might share preferences among foods. Yet very low correlations have been found between preference scores for common foods from students who have only recently left home and their parents (Rozin, 1991).

A major flaw in these studies is that the hypothesis has not been tested scientifically. A score for preference, liking or pleasantness of a named food, or a choice among food samples, does not measure what is preferred about the food. Each food is preferred for the levels of its attributes. That is, each family member has an ideal point and a differential sensitivity for each sensed and conceptualised characteristic of each food. At the very least, a familiar branded product or a sampled variant of a food will have an overall distance from the ideal of that food for each person in a particular context of use, involving social and somatic influences as well as sensory factors. It is these measures of the performance of preferring one material over another that should be tested for family associations, not the raw preference scores (cp. Guidetti, Conner, Prestwich & Cavazza, 2012; Pliner, 1994).

Again too, it may be more productive to measure each person's current frequency of each eating and drinking habit. That is where the preferences come from, during lifelong development through successive interactions between genomics and upbringing. Furthermore, differences between parents and offspring in habit frequency might be a rather specific indicator of which environments they have not shared.

Ingestive Appetite and Food Preference Responses

A scientific theory cannot be tested effectively until the terms in which it is formulated are empirically realistic. The investigation of chemosensory and other influences on ingestion has been greatly weakened by the assumption that differently worded ratings or differently named intake tests refer to distinct influences on ingestion. When that presupposition is tested on the different measures, the evidence shows that the various phrasings refer to one and the same phenomenon – the current tendency to take a mouthful of the food on offer.

Hence, outputs by themselves cannot differentiate among different inputs or mediating processes. Each proposed influence on preference or appetite has to be measured, as well as an integrative output such as disposition to accept the item in a specified context.

Sensations or Sensed Characteristics?

A rating by itself does not measure experienced sensations, contrary to the claims for magnitude estimation (Stevens, 1957) and indeed by the founder of psychophysics (Fechner, 1860/1996). Ratings do not achieve perception either: the evidence of perceiving comes from the relationship of the ratings to sources of stimulation to the senses (e.g. Shankar, Levitan, Prescott & Spence, 2009). Measurements of chemical concentrations are needed as well as all-or-none or graded responses in order to have the data on which to justify a claim that either chemosensory perception has been achieved or a taste or aroma sensation has been experienced.

Moreover, instead of being either an objective response to sweet constituents or a subjective expression of the experience of a sensation of sweetness, the rating of how sweet a sample is can reflect the use solely of the verbal concept of being 'sweet.' The tested sample may merely be put implicitly in a place along a graded series of named foods, such as from honey though chocolate, banana and apple to bread. Other processes that might generate a rating are describing (e.g., as being as sweet as a ripe banana) and unconscious sensing (e.g., an effect of sugar on preference without activating the concept 'sweet'). The distinctions among these various cognitive processes can be made by exact calculations from the raw data when an individual makes one or more analytically relevant ratings as well as rating overall preference (Booth & Freeman, 1993; Booth, Sharpe, Freeman & Conner, 2011e).

Preference or Appetite?

Acceptance is an act of the moment, whether the response is the physical movement of a piece of material or the symbolic expression of the disposition to do so (rated preference). The mouthful or the rating is subject to present influences. The observation can be assumed to generalise only to circumstances where the influences are identical.

Hence no intake test or rated acceptance can measure the palatability of a food because that means that the food has a constant relative acceptability at all times and in any context, which has long been known to be untrue (Booth, 1972a, 1990; Booth & Davis, 1973; Cabanac & Duclaux, 1970b; Duclaux *et al*., 1973; Rolls *et al*. 1979). Understandably therefore, many participants get confused when asked repeatedly to rate how "palatable" a food is, rather than how pleasant it is at each moment (Yeomans & Symes, 1999). Pleasant, liked, preferred, or attractive can all mean the disposition just at that moment in those circumstances. The numbers do not become a measure of a context-free palatability because an investigator assumes that they are. Simply not wanting more of a food right now does not make it any less possible to enjoy the food on other occasions.

Indeed, literal palatability clearly does not exist. Acceptance of a food is highly contingent on circumstances that vary by the minute within a meal and after an hour or two later. Those people who love steak cannot tolerate it as a second dessert, even if they have had no steak for days or weeks. Pieces of candy become quite boring if they are all the same taste, smell and colour (Rolls *et al*., 1979). At the most, a subset of people in a community may have a fairly stable hierarchy of preferences among foods for each particular use, e.g., one rank order at breakfast, another when snacking on the move, and yet another in a main evening meal. Such survey numbers should not be expected to contribute to quantitative accounts of chemosensory influences on ingestion. Rather, if such data are needed, they should be aggregated from representative samples of what individuals prefer in commonly occurring situations.

It follows that daily intakes of foods or the sizes of test meals that constitute nearly all of the published data on food consumption tell us almost nothing about measurable influences on eating. Meal size is a mere physical epiphenomenon accumulated from a large number of cognitively discrete actions, with changing sensory, social and somatic determinants across the minutes spent eating. Cultural appropriateness and physiological state do not have fixed influences either. Their effects depend on how they have interacted with each other and all the other influences on similar past occasions in the individual's life.

It follows also that important information about physiological influences on eating can be obtained from intakes of an unattractive food, so long as presented when the hypothesised signal is operating (e.g. Booth *et al*., 1970a,b). Indeed, intake from a buffet of diverse and tempting foods could well be insensitive to a physiological signal of appetite or satiety. Even more importantly, such tests make it impossible to analyse interactions among social and sensory factors that vary among those foods. It is far better to measure intake, portion by portion, of one food presented at a time that is regarded by the eater as appropriate to the occasion (e.g. Booth, Lee & McAleavey, 1976; Booth, Mather & Fuller, 1982; Dibsdall & Booth, 1996; Dibsdall *et al*., 1996, and in preparation).

Hunger is Appetite for Food

There has been a tendency to assign the terms 'hunger' and 'thirst' to bodily need for energy or water, respectively, or to require the presence of a physiologically signalled deficit in energy or water, while reserving the word 'appetite' for ingestion attributed solely to external factors such as the aroma of cooking or the sight of a beer or a soda. However, a half-full stomach and an incompletely covered plate can either inhibit or facilitate ingestion, depending on context of gastrointestinal hormones, eating or drinking companions, or other items to consume. There may be some force in the joke that optimists see a glass as half full while pessimists regard it as half empty. Yet the basic fact remains that they both tend to take more mouthfuls from the glass when the beverage is halfway to the top. What influences such mundane actions?

Hunger is not a purely bodily state that compels ingestion of food. Appetite is not a mental state driven solely by the sight or other sensing of food, drink, or other objects of desire. Rather, ingestive appetite is the cognitive-behavioural tendency to take a mouthful or more of a food and/or a drink, whatever the causes of that disposition are on a particular occasion. Appetite for food (usually in solid form) simply is hunger motivation. Similarly, thirst motivation is the appetite for a watery fluid.

Some people sometimes have rumblings or pangs in the upper abdomen when they want to eat, or a dry mouth or rough throat when they would like a drink. However, these sensations typical of hunger or thirst for some are not the same as the tendencies to ingest selectively. Rather, the individual's privately experienced epigastric pang has become associated by that person with the publicly observable desire for food.

The word 'sensation' should not be used to refer to a physiological signal either, especially in the metaphysically dualistic phrase 'central sensation' or the self-contradictory concept of an 'unconscious sensation.' Neural activation that stimulates appetite for foods or fluids is just that, whether central or peripheral, or conscious or unconscious. Metabolic or hormonal induction of food intake is not having a hunger sensation; there may be no awareness of the operation of the signal but only an increase in the motivation to eat. Osmotic or hypovolaemic stimulation of water intake is not a sensation of thirst. The osmoreceptors and baroreceptors generate central signals of water deficit, of which we may not be aware. Tactile receptors sensitive to drying of oral mucosa generate peripheral signals from reduced salivation. These signals are dispensable to the appetite for water but the dryness is likely to come to consciousness.

Words for Energy Intakes and Appetite Ratings

A great variety of words have been presented to human participants to assess the current level of appetite for food. People can be asked how hungry or full they are, whether they would eat a great amount, how strongly they want to eat or desire food, how pleasant it would be to eat a food, and so on. The answers have been claimed to measure distinct sensations, motivations, bodily states or social signals.

Many words have also been used in reports by investigators to label the weight of foods and volumes of drinks that have been swallowed (intakes) and the numbers assigned to positions between phrases about eating and drinking (ratings). Usually each label has been assumed to refer to the measure a different process influencing that intake or rating, such as an unconscious physiological signal, the subjective experiencing of a sensation, or unwittingly or deliberately following a social convention. Yet no evidence is provided the assumed process does indeed influence the numbers postulated to measure it, let alone more so than other numbers from other physical or verbal tests of hunger/satiety, i.e. the present strength or weakness of the appetite for food.

Contrary to all that, the first scientific step required for any multiple measures is to test for correlations between them, in order to check if they measure a single underlying variable. When that has been done for responses to a mouthful of a particular food, by itself or at one stage in a meal, the weights consumed and the words rated are found to be highly correlated (e.g., Booth, Mather & Fuller, 1982; Booth *et al*., 2011c; Hill, Magson & Blundell, 1984). Indeed recently it was found that the amounts of foods that a person wanted to eat at a particular moment correlated highly with the expected pleasantnesses of eating those named items (Booth, O'Leary, Li & Higgs, 2011c). That is, all the differently worded or labelled numbers measure the preference for that food in that context. If the dependency on the context is also characterised, such as a difference between the start and end of a meal, then the measure is of present appetite for that food. There is one single phenomenon, the acceptance of a tasted, seen or named food (or drink) in an implicit or explicit context of bodily and social signals.

The sign of a correlation is secondary: a negative correlation merely means that one of the two numbers reflects reduced acceptance. If that reduction of appetite comes from an effect of recent eating, whether sensory, social or somatic, then the rating or mouthful intake is a measure of the degree of sating of appetite for that food, or perhaps for many foods. The word "fullness" or "satiety" does not have to be mentioned in order measure the present depth to which appetite has been sated during or after a meal. The degree of specificity of the partly satiated state depends on further evidence, not mere assumption that the inhibition of appetite is specific to sensory modality, nutritional state or culinary category. Indeed an increase or decrease in rate of intake or appetite score may have nothing to do with appetite itself; it could come from a general excitement or lassitude, or even some malaise (Booth *et al*., 2011c).

For example, ratings of how "full" someone is at the time are negatively correlated with how "hungry" that person is then, or how much she or he "likes" a familiar food at that moment. That merely means the rater is less disposed to take a mouthful of that food. Saying "I'm full" is not evidence of a sensation of stretch in the upper abdomen, nor of how much food is in the stomach. Often it means merely the eater has had enough (of that food or of all food), i.e. has less of an appetite (Booth, 1976, 1990, 2009b; Booth *et al*., 1982).

Hence it is disastrously bad research practice to plot a separate time series of each differently worded rating. A single latent variable for strength of hunger and its sating should first be extracted from each of several representative points in time and that one number analysed and reported (Booth *et al*., 2011c). The only role for presenting data on differently presented tests of intake or variously wording ratings of appetite is to find out if one of the measures is consistently most sensitive to an influence that has been manipulated (Booth *et al*., 1982, 2010). This strategy is illustrated in this chapter for the cognitive machinery through which the chemical senses influence food choice and intake.

Words for Gustatory and Olfactory Intensities and Preferences

The same scientific mistake about alternative words for the same phenomenon has plagued research into sensory intensities and food preferences.

Intensities

Elaborate sets of vocabulary are presented to sensory panels without routine statistical checking of which words achieve distinctions among sensed factors. Each word is presented on separate point of a star diagram of rated intensities. Yet typically two or more of these words appear on effectively the same vector in graphs constructed from factor analysis or multidimensional scaling. This information should be used to weed out redundant terms for theoretical coherence and practical convenience. The reduced vocabulary then needs to be validated on measured variations among food samples of the sort to be assessed, not by training on an artificial model of the technically intended meaning of each term.

Statistical reduction of experts' vocabulary also uncovers the stabilities in their expression of the subtler distinctions that they have incorporated into their memory. Native speakers who eat the foods in life have already learnt the accurate uses of the words in their culture's language

(Wittgenstein, 1953). The word most heavily loaded on a principal component in factor analysis is therefore likely to be the most precise name for the actual sensed influence on perception.

Preferences

'Preference' is the scientifically most useful term for a set of influences on acts of eating or drinking. Influences can be cultural, via symbolic communications such as labels on foods, or interpersonal such as sight or knowledge of what someone else is eating. Hence influences from the sensed physicochemical characteristics of foods and drinks are more clearly identified by the term 'sensory preferences.' Strictly speaking, what is meant is a greater degree of acceptance of the 'preferred' item over alternatives. Nevertheless, the term 'relative acceptance' is too pernickety for general use. 'Acceptance' by itself is better used for the act of accepting a single item, as distinct from a factor influencing that physical or symbolic action.

Many other terms are used in ordinary English for preferring something, such as liking it, finding the item pleasant, having an appetite for it, desiring the item, wanting it, and so on. Sometimes these terms are assumed to refer specifically to the sensory component of preference but the evidence is that they all refer to the same phenomenon of responding to the cognitive integration of current social and somatic signals, as well as of sensed information.

Pleasant *versus* Pleasurable

A major disadvantage of words other than preference and acceptance is that they are taken by many people, including some scientists, to mean that something extra must be going on besides the observable preferring or accepting of an item. Preference is evident in the performance of selecting one food over others, more vigorous ingestive movements than in response to other foods, or rating a sample as more attractive than other samples. Perhaps the scientifically most important and longest standing example of misnaming of this greater acceptance is the term 'hedonic' (Booth, 1991).

This misconception of preference entered the research literature on behavioural nutrition in the applied area of designing military rations (Peryam & Haynes, 1957). The mistake now pervades the neuroscience of motivation, emotion and learning, and the social science of wellbeing, care of the needy and treatment of disease. The degree of preference for a food was assessed by checking one of a rank-ordered set of nine phrases from “like extremely” to “dislike extremely” (Peryam & Pilgrim, 1957). It is a still widespread mistake to use more than two anchor phrases (specifying a straight line against the determinants of preference; Booth, 2009b) because inevitably three or more anchors are unequally spaced (Jones, Peryam & Thurstone, 1955). Among early research users, these categories of food preference (and aversion) were called a 'hedonic scale' (Pilgrim & Girardot, 1952). That adjective comes from the classical Greek word for pleasure, *hedonē*. The presumption is that liking a food is the subjective experiencing of a pleasurable thrill while eating it. Unfortunately for ambitious suppliers of food, but perhaps conveniently for those who eat every few hours, sensual thrills from attractive foods are rather more unusual than those from erotic activity and other intense excitement such as a ride on a roller coaster.

The universal assumption that liking is a subjective experience rather than a public performance was exposed by the proposal of a Food Action scale (Schutz, 1965). The anchor words referred explicitly to observable activities with foods that indicated higher or lower rates of acceptance. Unfortunately the use of nine anchor phrases was continued, instead of just the two needed to keep responses in a straight line against levels of stimulation (Booth *et al.*, 1982, 1983, 2009b).

The error of equating preference with pleasure has been compounded by the verbal similarity between the word pleasure and the word used in a common measure of preference or appetite (and satiety) for an item -- its rated pleasantness (Booth *et al*., 1982; Rolls *et al*., 1979a). A whole theory of the biological roles of pleasure has been built on ratings of the pleasantness of gustatory and thermal stimuli (Cabanac, 1971, 1979). Any desired activity is a pleasant prospect. Yet, even when bodily sensations such as taste (or texture) are involved in the activity, as with eating and drinking, those conscious experiences need not be sensually pleasurable (Booth, 1991). Recently at last, the preference for a food and pleasure from the food have been dissociated experimentally (Booth, Higgs, Schneider & Klinkenberg, 2010a). It seems that revoltingly strong sweetness can activate some of the innate reflex to sweetness, so that the taster feels the characteristic movements in the mouth. Furthermore, in an adult such feelings can be pleasurable, raising mood and even creating a sense of smiling (Booth *et al*., 2010a). Further careful cognitive and electromyographic investigation is needed to determine if the some of the muscles that can be recruited by intense sweetness are the same as some of the muscles involved in a smile, and whether the pleasure comes from actual or incipient contractions or directly from the taste of sweetness.

Motivating Stimulus or Associative Reward?

The immediately observed motivating effect of a food stimulus is often called "food reward", without any evidence from later observations that the presentation of that stimulus had any associative effects, i.e. did any rewarding. The fact that a pattern of sensory input is preferred implies nothing about its contribution to learning through the reinforcement either of instrumental responses (reward) or of reactive movements to stimuli in classical conditioning (Berridge & Robinson, 2003; Booth, Jarvandi & Thibault, 2012; Epstein & Leddy, 2006).

The need for terminologically clarity is further emphasised by the demonstration that sweet taste by itself can serve as a reward in human subjects, creating an incentive stimulus out of a previously neutral odour (Yeomans & Mobini, 2006; Yeomans, Mobini, Elliman *et al*., 2006; cp. Stevenson, Boakes & Prescott, 1998). Furthermore, such reinforcing associations of cues with consequences has to be distinguished from associations between cues, which does not require reinforcement but can occur with habituation or familiarisation. We now turn to this learning of combined stimuli, starting with mixtures of taste compounds.

The Strength of an Influence

These problems with experimenters' assumptions about words are sidestepped in this chapter by starting and remaining with the phenomena to which the wordings put onto ratings or used to name intake tests are meant to refer. Whichever the wording chosen for a response, the stimuli that influence that rating are sought before proceeding any further towards even just summarising the data, let alone interpreting any response or claiming to observed any effect, quantitative (graded) or categorical (yes/no).

What matters is the strength of influence of a stimulus on a response, not a merely statistical prediction. These response-stimulus functions are familiar in biomedical science as dose-response relationships. If the amounts of the stimulus can be transformed into units that give a linear relationship to amounts of the response, the scientifically relevant measurement is the slope of the regression from stimulus levels to response levels (*b*), not the regression coefficient (ß). The reliability of the numerical value for slope needs to be assessed of course, but confidence limits are the best indicator of the precision of an estimate. P values depend on the number of data, whereas the only facts of scientific interest are the numerical values derived from the response-stimulus data pairs, however few or many there are.

Best of all would be a single measure of the strength of an influence on a response that takes into account both the value of the slope of response levels on stimulus levels and also the variability in level of response to each particular level of stimulus. Psychology has been sitting on just such a measure of causal strength for 170 years. The strength of influence of levels of a stimulus on a response is identical to the sensitivity of the response to the stimulus levels. E.H. Weber (1843/1996) measured the minimum change in touch on the skin that would change the response. For medium levels of stimulation, the fractional change was constant across a wide range of medium levels (for four tastants, see McBride 1983; for concentrations of a familiar mixture, see McBride & Booth, 1986). Weber and many others repeated the measurement of differential acuity in other sensory modalities and found that the fraction was constant across medium ranges of a particular stimulus. Weber's fraction divides the error in the responses by the slope of the response/stimulus function, generating a single number instead of three numbers, the slope and its two confidence limits.

The Weber fraction (or, strictly speaking, the ratio of levels that the fraction represents) is better known as the "just noticeable difference" (JND). However, distinguishing between levels of a stimulus has nothing to do with subjectively noticing a difference in strengths of a particular sensation. Preference or familiarity ratings can discriminate between stimulus levels, without ever mentioning sensory vocabulary. Weber's fraction is an objectively observed difference in level of response to a disparity between levels of measured stimulus, halfway between perfect discrimination when the two levels are far enough apart and the random responding that necessarily occurs when the two stimulus levels are identical. Hence it can be called the half-discriminated fraction (HDF).

For chemical and physical stimuli, the disparities are linear against response stimulation when the stimulus levels are plotted in ratios of the physical level, such as concentration. Concentrations of taste or smell compounds should therefore always be converted in logarithms. Otherwise a bowed curve is inevitable. Without the levels in logs, the distribution of slopes across individuals will be skewed as well.

Each Food Has a Different Taste

It is readily acknowledged that each species of food plant has a different aroma. Each fruit and vegetable emits a wide variety of volatile compounds and so could have a unique olfactory signature. It seems to be less widely appreciated that the taste of each food is also distinctive. How could that work when there are only a few distinct tastes to share among hundreds of foodstuffs? A key to the answer is that each taste presented by itself has at least about ten distinguishable concentrations, maybe twenty or more. Even from only four tastes, ten levels give a minimum of ten thousand (10^4) distinct combinations.

In reality, cooks and manufacturers have to spend a great deal of time and money to get each combination right. This is because eaters and drinkers are familiar with the correct mixture of levels of tastes, however conscious or not of the specifics they are (or what investigators of ingestive behaviour are aware of).

Tastes are the spice of life. Tastes wake us thoroughly in the morning and can send us to bed happy at night. From birth, the sweet taste helps us to love our mothers. The bitter taste protected young children who explored outside the encampment during our species' nomadic period, helping us to survive near extinction and then to expand around the globe. The sharing of tasty drinks celebrates the heights and soothes the depths. Seeking comfort repeatedly from chocolate or fruit cake can become part of counterproductive coping strategy. Yet the joys and satisfactions from tasty foods are also one of the happiest parts of regular daily life for many who live in richer countries.

The amount of a taste, not just the sort of taste

The first step towards understanding the roles of combinations of tastes in ingestion is to get away from the idea that the mixtures are just of the different tastes! This is not just the ordinary eater’s naivity. The research literature is dominated by hypotheses and interpretations about interactions between saltiness or sweetness with bitterness or sourness, for example, or a category of taste with viscosity, aroma, colour or whatever. To the contrary, what matters to eaters and to chemosensory science is the particular level of each taste in the ingested material.

It follows inexorably that, like all good things, there can be too much of a nice taste. This can be very obvious at a given moment, and quite easily rectified. Those of us who are used to unsweetened coffee can find the drink revolting when someone has added sugar without asking. We have come to find a moderate level of bitterness highly attractive alongside the aroma of coffee and perhaps a felt need for caffeine. Yet even those of us who like strong coffee can find too much in a brew and may dilute it with hot water, or even mask the taste with sugar or milk. For those who like lemonade, the taste of some acid is essential. Nevertheless, to make good lemonade, freshly squeezed lemon needs to be made less sour by adding water, not just sugar.

Ordinary eaters have learnt what levels work of the tastes in a familiar material. Unfortunately, so far most scientists have not. From molecular neuroscience to sensory testing in industry, and even in multisensory psychology, all the effects of the taste of sweet, bitter, sour, salty, savoury or any of the rest are treated as though they are continuously increasing quantities. Yet every effect of taste is tied to a particular amount of each taste, and indeed of an aroma, a mouthfeel, a colour and so on.

Levels of stimuli are also neglected by theories of learning, including accounts of learnt combinations of stimuli. Theories of the recognition of objects have the same defect, even those invoking the idea of a specific prototype for each object. All these approaches treat stimuli as categories, not gradations.

Which level?

Every taste (and any other feature) is needs to be scaled by how far it is above or below the learnt point for the combination it is in. That leaves a problem: how can distance from that standard level be measured? The answer is lies with Weber's fraction, the half-discriminated disparity (HDF) of a tastant's concentrations detected by preference or some other response.

The fractional increase in stimulus levels that just made a difference in the response of interest (e.g., how pleasant or sweet) can be calculated from a linear regression though the pairs of stimulus and response levels observed during an individual's session, as can also the level in the standard used by the participant to make those responses (Conner *et al*., 1988a,b; McBride & Booth, 1986; Torgerson, 1958). The concentrations of a taste or odour compound or a mixture in fixed proportions can then be converted into a scale of number of Weber fractions from the ideal point or familiar level.

Weber's fraction also solves the otherwise intractable problem of putting the concentrations of different compounds onto the same scale. Discriminative performance provides a common unit across and within tastes, and all other sensed characteristics of a food or drink. Whatever the chemical structure of the sweetener, and whether a small or a large amount is needed to provide the usual sweetness of a particular mixture, the disparity of the mixture from the standard can be measured in number of Weber fractions.

Scaling based on Weber's fraction has been grossly neglected because of the preoccupation of psychophysicists since Fechner (1860) with formulating a mathematical law that covers all levels of stimulation (Stevens, 1957). That is an impossible dream for two sorts of reason. The extreme limits cannot be in such a law because detecting the presence of a stimulus at low levels is a different task from discriminating between readily perceived levels (Laming, 1985, 1986, 1987) and at high levels the stimulus starts to saturate the receptors begin to saturate. A softer limit is that there is less experience of low and high levels of most stimuli than of the medium levels that commonly exist. Therefore performance outside the familiar range is less likely to be precise or even just uniform.

Number of Weber fractions from most familiar or preferred level is the basic scale for a response to any stimulus. Since all these response/stimulus relationships use same unit, they can interact with each other in a variety of ways within the mind (Booth, under review; Booth & Freeman, 1993). Hence Weber's fraction is the key that unlocks the mental processing required to have chemosensory preferences and consequent effects of the chemical senses on nutrition.

Cognitive Mechanisms That Convert Sensing into Ingesting

Causal Processes from Chemical Stimulation to Ingestive Movement

The rest of this chapter illustrates the experimental evidence for a mathematically precise account of the effects of perceived tastes and smells of foods and drinks on intended and involuntary consumption of selected items. The theory in its present stage of development is built up here piece by piece from quantitative evidence that has been published over the last three decades, plus some results in preparation for submission.

Central to the theory is the mathematical equivalence between the sensitivity of a response to differences in strength of a stimulus and the amount of influence that the stimulus has on the response. If preference responds to small variations in sweet taste, then sweet taste has a large influence on preference. In more specifically psychological language, the salience of a feature of a food for a response is the same as the attention paid to that feature by that response.

In other words, psychology's longstanding measure of differential sensitivity, Weber's fraction, is the key to working out the causal processes by which tastes and smells produce selective ingestion. Central interactions between taste receptor afferents are well recognised. These are particularly evident in subadditivity between responses to components of experimental mixtures of taste compounds. Various mathematical models of such 'mixture suppression' have been proposed, from a widely used cosine function (Cain *et al*., 1995) to parallel *versus* fan interactions in ANOVA (De Graaf, Frijters & Van Trijp, 1987; McBride, 1988, 1993; McBride & Finlay, 1990). Yet no specific mechanism has been proposed to justify either sort of calculation (see Schifferstein & Frijters, 1993). In contrast, the concentrations of the taste compounds in the tested mixtures can be scaled on number of discriminations from the standard in memory that was used by a response made to each sample. Then the observed values of that response can be predicted from causal processes specified by exact arithmetic (Booth, under review, a; Booth & Freeman, 1993).

First we consider the ubiquity of the phenomena that require scientific explanation.

Mixing It

Perhaps the most important fact about the sense of taste is that identifiable tastes always come in combinations with each other in life. Of course, tastes in food and drink also go along with the other senses -- aroma, colour, shape, seen and felt texture, and so on. Some interactions between the senses can be amazing (Spence, 2010). Yet equally extraordinary interactions occur all the time within the sense of taste. Stimulation of one type of gustatory receptor is almost always combined with stimulation of another taste receptor type, or even with two or three tastes.

These natural gustatory mixtures are very precise too. The tastes have to be balanced against each other, even when their overall strength is about right. Many eaters of fish and chips like to put their own salt and vinegar on the potato fries: their taste is not so nice when swamped in the sourness of vinegar or made far too salty. Those who take sugar in coffee, with or without milk, are quite particular about both the strength of taste of the coffee and the number of spoonfuls of sugar. This is an example of three tastes, too, because coffee tastes sour as well as bitter. Take note next time you have a drink made from ground coffee. What if it were too sour, even if you like strong coffee? Tea can go with lemon but coffee does not need it.

None of this has anything to do with aroma, colour, crunchy sounds or any other sense than taste. Nor is it in the outer reaches of creative gastronomy, or visual enough to matter in TV cooking competitions. It happens several times a day in everyone's life: talking often has to compete with taste for the occupying the tongue!

These complexities of the sense of taste and their many roles in everyday living create challenges and opportunities for all sort of cognitive processing, from physical information to social communication. Think of the mental mechanisms required to recognise each combination of tastes as appropriate to that food item and the dish it is in. Such cognitive science is way beyond the genetics and the neuroscience that deal with one taste at a time. Everyday taste cognition also flies well under the radar of the economics and the social anthropology of salt, sugar, oranges, chocolate and coffee.

Yet in the main, social and cognitive scientists consider tastes to be irrelevant to personal interaction, empathic perception, the acquisition of language, perception, memory, reasoning and almost everything else of academic and practical interest. A cognitive psychologist has been heard to dismiss such matters as a trivial job for the hypothalamus. Yet the taste pathways have much less influence on that region of the brain than on parts of cortex relating to actions, expectancies, and percepts integrated across all the senses.

To the contrary, sensory science needs to join the mainstream of research into the cognitive processes in physical and social perception and action. Familiar mixtures of tastes are a good place to start. Tasting with the tongue is as deeply involved in human culture and language as other human capacity alleged to be 'basic' and traditionally supposed to be wired into the brain by the genes. The neuroscience of the 'basic emotions' expressed in the face has been forced to go beyond locating each emotion in its own bit of the brain.

Similarly, the question is no longer merely whether there are four or five (or more) 'basic' tastes, each with its own type of receptor on the tongue and its own word in the English language. The whole idea of such labelled lines through the brain has broken down. Even a single nerve fibre going from the tongue to the brain can be activated by two or more types of taste receptor (Roper, 2007). Indeed, a taste bud contains multiple receptor types that are coupled to an afferent nerve by messengers between cells (Roper & Chaudhari, 2009; Tomchik, Berg, Kim *et al*., 2007). Hence, even the first relay in the pathways for gustatory information through the brain lacks the information required to identify a compound that stimulates a single receptor type.

Rather, the approximation to a one-to-one relationship between receptor type and verbal concept is a brilliantly flexible achievement by human societies in educating their youngsters into implicit understanding of the complex tastes of foods. We don't teach the meaning of "sweet" by giving some honey or sugar water to taste and saying the word. We use the word to warn a child that the fruit may not be ripe yet, for example, or to point out that no sugar is needed on the muesli because it contains raisins. The concept of sweetness emerges in such conversations, already defined by the contexts of its use (Quine, 1974; Wittgenstein, 1953). Sucrose is identified as sweet by the information from the hT1R2 receptors interacting deeper in the brain with social and physical information gathered via other senses in the past as well as the present.

Configured Ideal Points

Mixture Statistics

Even a mixture of molecules that all stimulate a single taste receptor type generates a severe scientific problem, with enormous practical implications. There is no mechanistic theory in general use for mixtures having more than one taste. Until recently, experiments on interactions between tastes (or odours) used mixtures of single compounds which had not been experienced by the research participants before entering the laboratory. Mutual suppression of intensities was almost universally seen, which could be fitted to a theoretically unspecified angle in a cosine function (Cain *et al.*, 1995). Intensification of intensity (synergy) was claimed in some special cases, such as glutamate and ribonucleotides (Yamaguchi, 1967).

When three or four arbitrarily chosen taste or odour compounds are mixed, the suppressive interactions become so strong that the components become difficult even to recognise (Laing, Link, Jinks & Hutchinson, 2002). The compounds can only mask each other (Cain *et al.*, 1995; Marshall *et al.*, 2006). The masking gets worse if configural learning is prevented by training to attend to one of the compounds (Kurtz, Lawless & Acree, 2009; Prescott & Murphy, 2009).

The effect was reduced by familiarisation with the mixtures and so it was suggested that learning to configure the separate tastes or smells could remove confusion among them (Laing *et al.*, 2002). A major review of the literature on recognition of odours concluded that each profile of receptors stimulated repeatedly stimulated receptors was stored in memory as a configuration that could be compared with subsequent mixtures of volatiles (Stevenson & Boakes, 2003).

A theoretically cogent statistical theory of configural learning has been proposed (Pearce, 1994, 2002). However it has not been brought into use within research on the chemical senses. Norm-zeroed multiple discrimination theory provides a simple arithmetic of learnt configural stimuli (Booth, under review, a; Booth & Freeman, 1993). The remainder of this chapter is devoted to illustrating analyses of data in accord with this quantitative mechanistic theory. The approach was first applied to mixtures of taste compounds. Indeed it developed from work on variations of concentration of a single taste compound in a familiar context, rather than in an unfamiliar pure solution (Booth *et al.*, 1983). Contextual influences of various sorts have long been recognised in food research; indeed they have sometimes been called cognitive effects (Davidson, Linforth, Hollowood & Taylor, 1999; Pfeiffer, Hort, Hollowood & Taylor, 2006). Nevertheless, the concept of context has been vague and contextual effects poorly specified. Indeed, context has sometimes been dismissed as a nuisance variable.

Scientific Measurement of Context

The first measurement of the role of the chemical senses in preferences for familiar foods and drink varied the concentration of a single taste compound -- sodium chloride (Booth *et al.*, 1983). The well learnt contexts tested were plain white bread or tomato soup eaten by itself.

The strength of the taste of salt in each sample of bread or soup was rated relative to the individual eater's most preferred strength held in long-term memory. The key anchor phrase on the array of positions to choose as the response was "just right for me." It is crucial that the participant is referred to a point on linear array involving a single objective concept, such as an act of acceptance or the taste of salt.

Much research practice treats ordinary people as incapable of making such quantitative judgment on familiar matters. Hence only a choice of boxes to tick is provided, for agreement with one of the more or less complex phrases set against each box. Suitably chosen phrases can be arranged in a sequence of decreasing strength, e.g. from "like extremely" to "neither like nor dislike" but the responses are then only ranks, not quantities. They represent only ranges of preference, of indeterminate width and hence unknown borders between ranges. The "just right" point was modified in that approach to a "just about right" range. The consequences have been disastrous for theoretical understanding of the cognitive approach and to practical use of data on preferences, sensed characteristics and marketed attributes (Booth & Shepherd, 1988; Booth & Conner, 1991, 2009).

In fact, anyone who watches TV talent shows is fully capable of constructing scores from zero to ten (with halves too, and even decimal fractions). Percentages as well are readily handled by tennis fans examining champions' match performance of points one on return of serve, and so on. Only two scores should be anchored because a third anchor is at risk of unequal spacing from the other two anchors. Then unlabelled boxes, hatch marks on a line or a row of integers can be provided for the response. The extraordinary procedure of measuring distances along an unstructured line is totally unnecessary (Bowman, Booth, Platts *et al.*, 2004).

The theoretical zero point for discriminations by degree of preference is the most likely choice, i.e. a rating at the "just right" anchor point. However the zero that the rater needs in order to make genuinely quantitative judgement can be absence of preference or of the characteristic being assessed. No sample should be presented that risks being rated close to zero, because that is liable to induce a floor effect and departure of the response/stimulus graph from linearity.

The concentrations of each taste compound varied and the ratings of closeness to its ideal level (or to the ideal version of the undescribed food) can then be fitted to the contextualised hyperbola (Figures 5 and 6). The key principle is that one peaked causal/discrimination relationship is always in the context or one or more other peaked response/stimulus functions. Since each response/stimulus relationship is linear in number of Weber fractions from the ideal or familiar point, the data-points theoretically form an isosceles triangle, having the same slope (of opposite signs) on each side of the apex (Booth & Conner, 1991). If two such triangles for the same response at right angles, with a single apex, the responses to the mixtures of two influences form a cone, with the data from each sample plotted at a point on its surface. Furthermore, if the variations in level of one component are tested with the average of levels of the other influence being off the ideal or usual point, then the peaked function will be the surface of a cone on a vertical cut down the side of the cone away from the peak. The shape of this conic section is a hyperbola. Hence the responses to a sensory influence should always be fitted to the formula for a hyperbola, $y^2/x^2 = 1$. When the context for each tested sample is near enough ideal in all respects, the fitted hyperbola will approximate to the isosceles triangle to which the limbs of the hyperbola asymptote. This calculation from the raw data gives functions like those in Figures 5 and 6, for sugar and acid in a fruit drink and for caffeine in coffee (other constituents of which taste sour as well as bitter).

The hyperbola for a single stimulus influencing preference follows from the mere presence of another taste. Alternatively, the whole context can be integrated into another single stimulus dimension. When these two dimensions are plotted at right angle in the horizontal plane (x and z axes), with the response dimension plotted vertically (y axis), the result is a cone with the data from each sample plotted at a point on its surface. There need be no systematic variation in any element of the context. The mathematics follows independently of data on any other component of the mixture. For example, nothing needs to be known about other constituents of coffee in order for it to be correct to fit a hyperbola to responses to a coffee drink in which in caffeine levels were varied.

In this way, norm-zeroed discrimination scaling directly generates a mathematically exact theory of context (Booth & Freeman, 1993). When one or more samples is close enough to the most preferred level, the peak of that hyperbola can be interpolated (as in five of the individuals in Figure 6). The average distance of the whole context from ideal is then the distance from that rounded peak to the peak of the triangle formed by tangents to the hyperbola. The size of the defect is measured by the distance between the hyperbola and the triangle, either between the peaks in response units or horizontally in number of Weber fractions. A source of a defect in context can be sought by varying a suspected cause and interpolating its average levels in samples showing the defect into the scale of its influence on preference.

Interactions Among Separate Influences

The cone is formed by preference responses to different levels of a single influential stimulus in any sort of context. If a second stimulus is varied independently of the first one, the cone provides a default model for a response that varies among those mixtures of the two stimuli distinct stimuli. For example, two compounds might stimulate distinct types of receptor (as in Figure 5) or two distinct profiles of multiple receptor types, such as bitter receptors or olfactory receptors.

The formula for the distance of the theoretically maximum response from the response to a mixture of two different sources of stimulation, at distances A and B, is $(A^2 + B^2)^{0.5}$ in accord with Pythagoras's theorem. This square root of the sum of squares extends to familiar mixtures of three, four or more distinct stimuli, because Pythagoras is also valid over any number of dimensions (although such 'hypercones' cannot be visualised).

Identical or Configured Influences

There are two ways in which distinct sources of stimulation can operate cognitively on a response on a single dimension (or, in terms of communication theory, transmit information from multiple input patterns to an output pattern over a single channel). The two stimuli may act on the same type of receptor. Hence the information provided by that route cannot enable any response to distinguish between its sources. This unidimensional mental mechanism is used in this chapter to test if two taste compounds act on the same receptor. The discrimination distances simply add, rather than acting orthogonally.

An alternative is that learning creates a single dimension (or channel) from two stimuli that act on different receptor types, intramodally or intermodally (Booth, 2013). Exposure to a particular mixture of distinct taste and/or odour compounds can set up a standard or norm in long-term memory in which those levels of the components are treated as a unity by the learnt response. In effect, the particular mixture becomes a new stimulus, distinct from any components of the mixture, although each component may retain control of a response distinct to it. The particular combination of levels become a unique configuration controlling the learnt response. When this emergent sensory influence comes from a binary mixture, it functions as a "third stimulus" to the response. This perceptual achievement is used in research into animal learning as the criterion of configuring among distinct sources of stimulation (Rescorla, 1973).

Like any other learnt stimulus, departure of any component's level upwards or downwards from the learnt set of levels weakens the response. Such a test mixture has some dissimilarity from from the configured mixture (Shepard, 1958). This difference in performance on a combination of stimuli is the basis for a leading theory of less than perfect configuring (Pearce, 1994), developed for categories of stimuli potentially having quantitative features (George & Pearce, 2012; Pearce, 2002).

The arithmetical formula predicting the response to such mixtures is changed by configural learning from root sum of squares to straight summations of the discrimination distances from norm, i.e. (A + B) for a mixture of A and B (Booth & Freeman, 1993). The same formula tests for a receptor type stimulated by two different compounds, even when one or both compounds also stimulate other types of receptor.

Gustatory Configurations in Ingestion

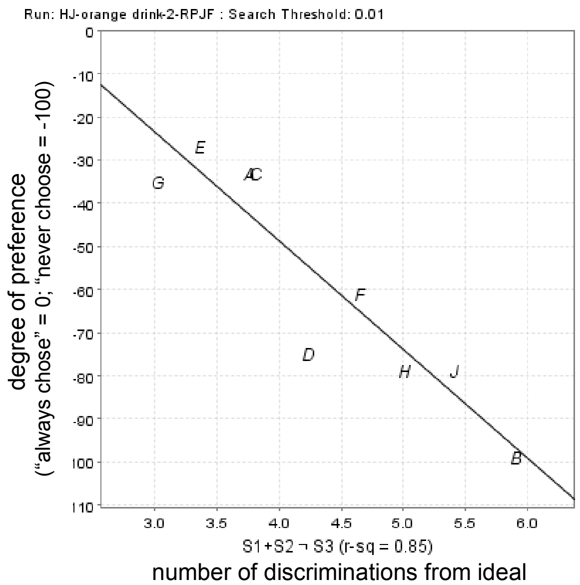
The Balance of Sweet and Sour in Oranges

The taste of the flesh of a ripe orange is one of the best models for the study of gustation in real-life ingestive behaviour. Peeled whole oranges are a widely consumed food. Juiced whole oranges are even more widely used as a drink, usually unmixed with other juices and without addition of sugar or other materials. A long-life variant of fresh orange juice is made by condensation, for dilution back to strength on use; that processing is liable to change the aroma but not the taste, texture or colour. Filtered condensate is made into a cordial ('orange squash' in the UK) which is popular among children after dilution to taste.

An orange-flavoured drink, like orange soda without the carbonation, can be made by dissolving a mixture of orange-like colouring and aroma in mains water, adding fruit acid, table sugar and/or intense sweetener, and a clouding agent to replace fragments of orange. A still, clouded orange-flavoured drink, using sucrose and citric acid as tastants, is widely available in the UK from cold drinks vending machines. Frequent users can therefore be tested on a familiar sweet drink which is also sour, at the balance of intensities expected of orange flavour.

In one series of experiments (Freeman *et al*., 1993), we sought evidence that sweet sugars act on one sort of taste receptor while fruit acids stimulate another receptor type (or more than one).

Figure 8. Cognitive integration (possibly unconscious) into initial ratings of closeness to most preferred quality (R1) for samples of a familiar orange-flavoured drink (“always/never choose”: $r^2 = 0.85$) of the stimulation of one type of taste receptor by sucrose (S1: 48% contribution) and fructose (S2: 41%) and of a different receptor type by citric acid (S3). Data-point letters: sequence of presentation of samples, from A = 1st to J = 9th. Malic acid (S4) was also varied among the drink samples but its stimulation was not integrated into preference by this assessor (coded HJ) in this second replicating session (drink-2), conducted by Richard Freeman (RPJF). During search for the best account of the variance in preferences, a more complex cognitive model was accepted as better if the increase in r^2 was greater than 0.1. Graphic output from a run of the recently programmed tool, Co-Pro2.29.



The only other evidence that different sugars act on the same taste receptor (now known to be oral hT1R2) used complex designs and calculations to uncover concentrations of pairs of sugars that could not be discriminated (Breslin, Beauchamp & Pugh, 1996; Breslin, Kemp & Beauchamp, 1994). That approach is not applicable to mixtures of tastes or to single compounds that possess more than one taste, such as a sweet and bitter amino acid, or have any other sensory effect, such as the difference in osmotic pressure between equally sweet solutions of a monosaccharide and a disaccharide (Breslin *et al*., 1996).

In contrast, discrimination from norm can readily pick out compounds that add stimulation to one type of receptor from different compounds (or the same compound) stimulate another receptor additively. Illustrative findings are summarised in a graph calculated directly from the raw data gathered in an individual’s session assessing variants of the vended orange drink. In this experiment we used quaternary mixtures close enough to the sweetness and sourness of the marketed drink to be within the region of constancy of Weber’s fraction, halfway between perfect discrimination and random responding.

The learnt norm that the assessors were asked to use was the most preferred taste of the familiar drink. That is to say, an assessor was asked to judge where each sample was between being chosen every time and never being the choice. The mixtures were tailored to each assessor's range of tolerance as it became apparent from the first two or three samples, in order to avoid ratings close to either extreme.

Direct Stimulation of Preference

In one assessor, preferences in the second session were directly driven by stimulation of receptors specific to sugars or acids (Figure 8). If no concepts of sweet or sour taste were activated, then these influences on preference could have been subconscious. In the cognitive processing, aware or unaware, that was most predictive of rated preference ($r^2 = 0.85$), distances from norm of the levels of sucrose and fructose were added together (S1 + S2). In other words, the information from each of the sugars was transmitted over a single channel from the receptors in the mouth to the decision where to place the degree of preference for each sample between always and never choosing each variant of the drink.

Stimulation from citric acid (S3) had an independent influence on preference (Figure 8). That is evidence that gestation depends on at least one receptor for acids which is different from the receptor for sugars. No direct effect of malic acid (S4) on preference was seen in this most predictive model of the session's processing (Figure 8). Hence this particular set of data happened to provide no test of the hypothesis that the two acids act on the same receptor.

Another assessor did provide such evidence in the third session on these quaternary mixtures (Figure 9B). The first session, however, again showed addition of the two sugars' distances from norm with a separate effect of citric acid alone (Figure 9A).

Sensations *versus* Thoughts Controlling Preference

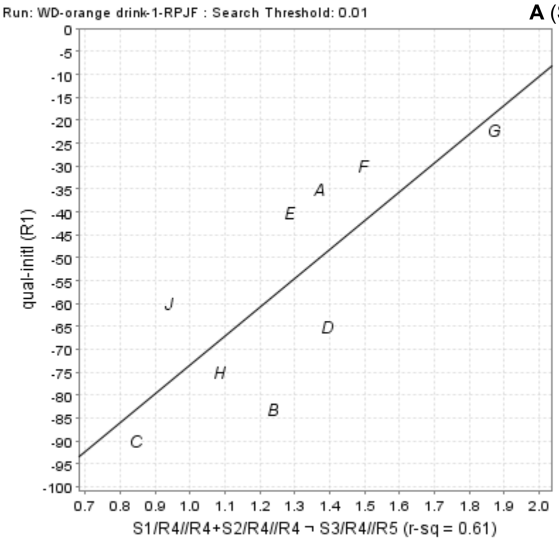
In both these sessions with this participant, the effects of the taste compounds on preference were indirect. Indeed, they were mediated by processes even deeper in the mind than conceptualising the stimulation (S/R), i.e. describing a feature of the drink.

The best account of the data from the first session was a set of S/R//R processes (Figure 9A). Such a conceptually modulated (//R) description (S/R) gives the meaning or intention of the modelled response – in this case the degree of preference for each orange drink sample containing a tested mixture (R1). On this evidence, the session was dominated by two reasons for choosing a sample. One reason was a configuration summing (+) the closenesses to an orange drink that is appropriately "sweet" (//R4) described as both sweet sucrose (S1/R4) and sweet fructose (S2/R4). A more minor reason was an appropriately "sour" taste (//R5) in sweet citric acid (S3/R4). This description of citric acid as sweet (S3/R4) rather than sour (S3/R5) could be interpreted as 'unsweet' because the level of the acid can be recognised from its suppressive effect on the taste of sugars also included in a drink that is conceived overall as sweet.

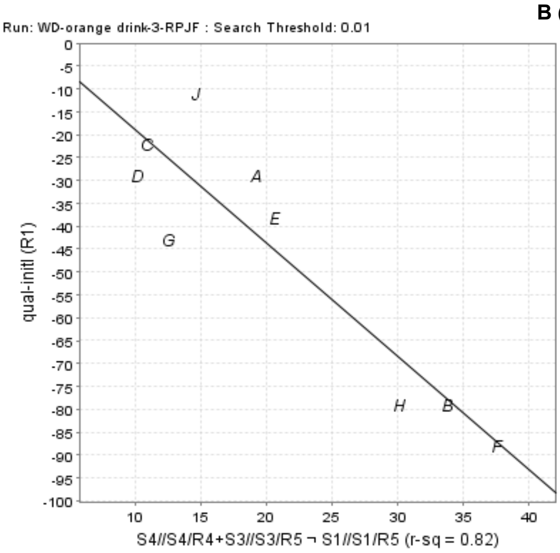
In the third session (Figure 9B), there were three sorts of modulation of stimulation (S//) by a descriptive process (S/R), i.e. perceptual processes or sensations (S//S/R). The major taste sensation was a configuration (+) of two processes. The greater contribution came from the process of receptor stimulation by malic acid (S4) being described as sweet malic acid (S4/R4) – another case of recognition by suppression. The smaller contribution to the complex sensation was a process of describing citric acid (S3) as sour citric acid (S3/R5), i.e. perception of the acid

Figure 9. Preferences for variants of a familiar orangey drink decided through complex meanings or sensations in the first and third sessions of one assessor (coded WD). The cognitive integrating processes were the assessor's objective achievements but they were also subjectively experienced, since they involved the concepts of 'sweet' (R4) and 'sour' (R5) that were used in other ratings of each sample for taste intensities. S1 = sucrose. S2 = fructose. S3 = citric acid. S4 = malic acid. Init-qual (R1) = the first rating of each sample, at a freely selected point between the anchors "always choose" (0) and "never choose" (-100). In Session 1, the concept of sweetness gave meaning (//R4) to the description of each sugar as sweet (S1/R4 and S2/R4) within a single reaction (+), simultaneously with a different meaning (¬) of sourness (R4) to s suppression of sweetness by citric acid (S3/R4). In Session 3, description (S/R) of malic acid (S4) as (un)sweet (R4) generated a sensation (S//S/R) from stimulation by malic acid (S//) that was the same (+) as a sensation in which citric acid stimulation was described as sour citric acid (S3/R5), alongside a separate sensation from stimulation by sucrose described as the sourness (suppression) of sucrose.

A (Session 1)



B (Session 3)



as sour. There was a separate contrition from a simple sensation in which sucrose (S1) was described as the sourness of sucrose (S1/R5). This is the converse of the suppression (S3/S4) seen in the first session.

One of the remarkable aspects of this approach to measuring the determinants of preference is the diversity of cognitive hypotheses that compete as explanations of a modest amount of data from a single session with one individual, using only a total volume which is close to that usual for the drink. Norm-zeroed discrimination is a highly economical way of reading the mind while the chemical senses are exerting their usual influence on ingestion. This fact in itself is evidence that these analyses get very close to what is actually going on as we eat and drink. Less precise suggestions have recently been made from much more complex data. The ratios of components have been seen to be important to the combining of elements into a recognisable mixture (Jinks & Laing, 2001). The Weber fractions of components have been found to affect the quality of the mixture (Le Berre, Béno, Chabanet *et al*., 2008).

Mono-Sodium Glutamate: the Complex Savoury Taste

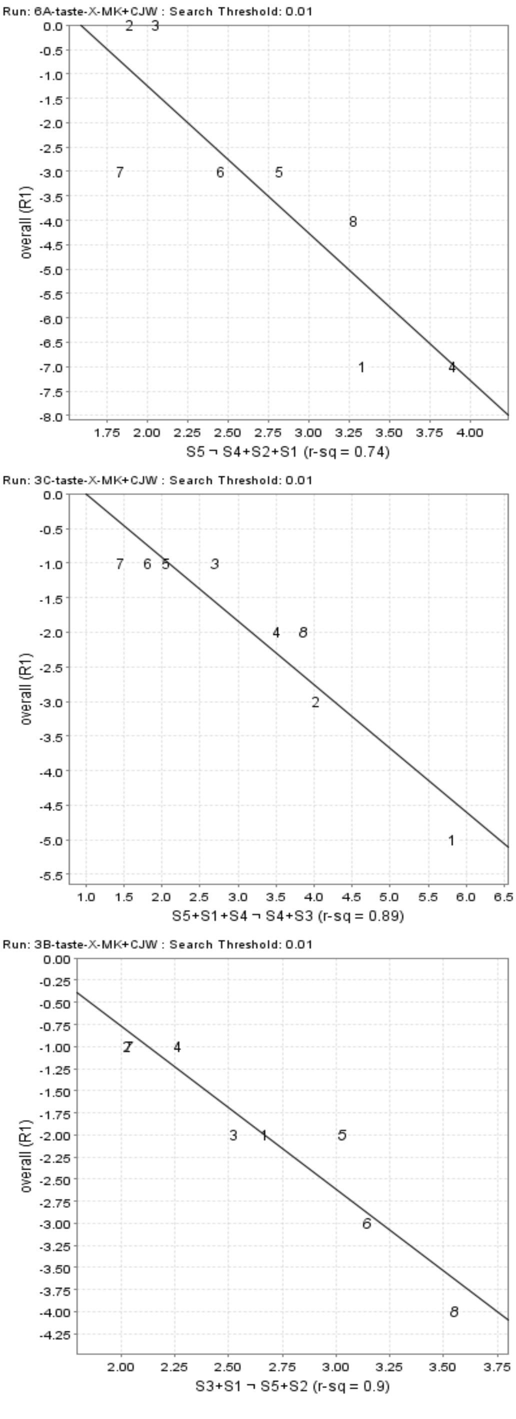
Another example of the power of norm-zeroed discrimination scaling within individuals exploited the approach's capacity to tackle the problem of a single chemical compound having multiple tastes. The monosodium salt of glutamic acid (MSG) tastes both sweet and bitter, as do many amino acids. Since one of the two carboxylic acid moieties has not been neutralised, MSG also tastes sour. Its sodium content of course makes MSG taste salty as well. If concentrations of the five compounds, MSG, sucrose, caffeine, citric acid and sodium chloride are varied independently in a familiar glutamate-rich food, the assessor has the opportunity to show that MSG stimulates each of the four classic types of receptor by adding its discrimination distances from norm to those of each of the other taste compounds. (Caffeine would not work in this design if MSG stimulated a different profile of the T2Rn ('bitter') receptor types. Nevertheless, caffeine has a broad profile (Behrens, Foerster, Staehler *et al*. 2007), and is widely used in coffee, tea and other drinks.)

Such a four-dimensional discrimination model was found in pilot tests of mixtures in tomato and chicken soups (Freeman *et al*., 1993). That finding has been replicated and extended using mixtures of all five compounds in tomato juice (Booth, Konle & Sharpe, 2008; Booth, Freeman, Konle, Wainwright & Sharpe, 2011a). The taste of a tomato is dominated by its large content of the mono-hydrogen glutamate ion in MSG. Tomatoes also contain some sodium ions of course. Marketed tomato juice has a large amount of salt added. Evidence that the identical sodium ions from the chloride and glutamate salts act on the same receptor helps to validate the approach.

Different assessors added discrimination distances of MSG to the distances from norm of different pairs or trios of the other four tastants (Booth *et al*., 2011a). Nevertheless, the four types of simple taste stimulated by MSG were covered across the set of assessors. That result is illustrated here for two overlapping trios and a different pair (Figure 10).

The component S4 + S2 + S1 in one session (top panel, Figure 10) showed that information from citric acid (S4) and sodium chloride (NaCl: S2) was transmitted to the overall taste of tomato juice through the same channel as MSG (S1). The combining of MSG with NaCl validated this

Figure 10. Three cases of stimulation by MSG of receptors for stimulants of a single taste (salty, sweet, sour, bitter). Data-point integers: sequence of presentation of samples. R1 (y axis): overall similarity to tomato juice (0 = no difference). Model's number of half-discriminated fractions from familiar juice for each sample (x axis). S1: MSG. S2: NaCl. S3: sucrose. S4: citric acid. S5: caffeine. +: stimulation of receptors that are combined in the taste of MSG. ¬: stimulation of separate receptors. Data collected by Melanie Konle and Clare Wainwright.



interpretation because the sodium ions from MSG and NaCl are of course identical and so must be undistinguishable. On that basis, the evidence from this session is that the acid moieties in the glutamate ion stimulate the same receptors in the (tricarboxylic) citric acid. That is unsurprising since both donate protons.

One session in another assessor (middle panel, Figure 10) had the component S5 + S1 + S4, where S5 is caffeine. Hence MSG stimulates caffeine receptors as well as citric acid receptors. This session's data were fitted well by inclusion of a second component (S4 + S3), combining stimulation by citric acid and sucrose. The obvious explanation of this transmission of information from two types of taste receptor along the same channel is that they are both stimulated by glutamate. So, even though MSG itself was not included in this component, these data provide indirect evidence that MSG can taste both sour and sweet (Booth *et al*., 2011a).

The previous session in the same assessor (bottom panel, Figure 10) combine stimulation by sucrose (S3) with MSG (S3 + S1). This is direct evidence that MSG stimulates the sugar receptor. A separate component summating stimulation from caffeine and NaCl would be explicable by MSG having a bitter taste as well as a salty one.

In short, the results of this experiment on mixtures of five taste compounds in a familiar drink shows that norm-zeroed and contextualised discrimination scaling can identify concentrations of compounds that match exactly (are not discriminated from each), even when one compound stimulates more than one type of receptor. There is no need for tortuous cycles of testing for mismatches between a standard sample and the samples that try to mimic it exactly. Familiarity with the real-life item provides a standard in memory for judgments of any degree of dissimilarity from the experimental items. The resulting data provide not only Weber's fraction for each varied component but also its point of equality with that learnt norm.

Amino Acid Detectors in the Mouth and Brain

The above findings on MSG say nothing about the existence of a glutamate taste receptor on the human tongue (Li, Staszewski, Xu *et al*., 2002). The question they raise in whether such a receptor has been needed for human survival. Free and combined glutamate is a major source of nitrogen in the diet, but it is a non-essential (dispensable!) amino acid. If we need a detector for the tastes of the amino acids that are essential to the diet (i.e., cannot be synthesised in the human body), then oral receptors specific to at least several of those are needed, such as methionine, creatine, leucine or phenylalanine. There is (so far) no evidence for these.

In fact, the necessary detector has recently been identified, as long suspected, in the protein-synthesising machinery of a specialised region in the forebrain. In pyriform cortex in rats, a local deficiency in one or more of the essential amino acids blocks transfer RNA (Gietzen & Aya, 2012). This creates an adverse neural effect which rapidly conditions sensory aversion to a recently ingested novel food. In addition, a balanced supply of amino acids, restoring protein synthetic function, conditions preference to the most recent smell, taste or flavour of food in rats (Booth, 1974; Booth & Simson, 1971; Simson & Booth, 1973), sheep (Villalba & Provenza, 1999) and people (Gibson, Wainwright & Booth, 1995).

Furthermore, the preference conditioned to any flavour by repletion of protein, or an essential amino acid, can become configured with the pyriform signal or some other effect specific to depletion of essential amino acids. This learning process elaborates the selecting among foods into a protein appetite, i.e. an increase in sensory preference when in physiological need. Both rats (Baker, Booth, Duggan & Gibson, 1987; Booth & Baker, 1990; Gibson & Booth, 1986) and people (Gibson, Wainwright & Booth, 1995) learn a protein-specific appetite – that is, a learnt facilitation of ingestion by both the flavour and the state of need for protein which have been followed by repair of that need.

The complex taste of glutamate may be a natural sensory component of the learnt appetite for protein (Gibson *et al*., 1995). Normal foods that are rich in good quality protein (balanced in essential amino acids) often contain high levels of free glutamate and other amino acids. Hence this distinctive sensory cue could be conditioned in combination with signals from lack of protein that can develop within a few hours after a protein free breakfast (Gibson *et al*., 1985). Furthermore, there is evidence that older people with low blood urea nitrogen may acquire a taste for hydrolysed casein, despite its bitterness and foul odour (Murphy & Withee, 1987).

The Savoury Complex or a Fifth Simple Taste?

Presumably the glutamate receptor on the human tongue has made it easier to recognise sources of protein. Glutamate is not an essential amino acid but it is the most abundant component of proteins and also occurs uncombined with other amino acids in the fluids of vegetables as well as meat and fish. However most amino acids taste sweet and/or bitter and those with two acid groups, like glutamic acid, taste sour as well. Monosodium glutamate (MSG) stimulates all the other four types of taste receptor. Hence it was proposed that those of us think of the course of meat and vegetables in a main meal as savoury transfer that concept to the complex mixture of tastes in the free glutamate ions and also the sodium ions inherent in those foods (Freeman *et al*., 1993). That is, the taste of glutamate could create a learnt configural stimulus from mixtures of sugar, acid and whatever type of bitter substance stimulates a profile of those receptors similar to that by amino acid, plus the salt that is there as well.

Such configural norms should allow better perceptual performance than does recognition of the components. So it proved for the savoury taste of tomato juice (which has salt added to the juiced tomatoes). The Weber ratios of distances from the familiar mix of tastes achieved that were achieved by ratings of how sweet, sour, bitter and salty were better for the MSG in tomato juice than they were for added table sugar, fruit acid, caffeine and salt.

All Sensory Vocabulary is Learnt Social Names

Our tongues have receptors for the commonest amino acid, glutamic acid (with one of its acid groups ionised), as well as receptors for salt, sugar, acids and a wide variety of poisons in plants. This finding has added some strength to the proposal that there is a fifth 'basic taste.' Hitherto that idea rested mainly on the ease with which the taste of MSG could be distinguished from the tastes of non-amino carboxylic acids, sugars and bitter substances. However, all sorts of mixtures are readily distinguished from each other and from their components. If as much effort for MSG as for the tastes of seafood delicacies were put into trial-and-error matching of a natural taste mixture to an artificial mixture (Fuke & Konosu, 1991), a taste indistinguishable from MSG could very likely be created. In any case, it is now clear that a theoretically appropriate approach enables matching mixtures to be interpolated from analyses of data from a single set of appropriately designed samples.

British English has long had the word 'savoury' for the vegetables and meats in which glutamate is at high levels, as well as the worldwide English names 'salty', 'sweet' (or 'sugary'), 'sour' (or 'acidic tasting') and 'bitter' for stimulants of other types of gustatory receptor. The malleability of this cultural end of those alleged 'labelled lines' has been neatly illustrated by a superb public responsibility marketing operation by the biggest manufacturer of the flavouring compound, monosodium glutamate. By promoting research into the taste of glutamate, the company in Japan has managed to displace the word 'savoury' in the English-speaking scientific community by a word they invented, 'umami,' which is closely related to the Japanese word for delicious. How could there be a problem for consumers with a food additive that has its own receptor on the tongue with molecular genetics for the membrane protein? The MSG itself cannot be blamed if some cheap restaurants pour excessive amounts on their food, or some of their customers have bad reactions that they incorrectly attribute to the meal (Knibb & Booth, 2011; Knibb, Booth, Armstrong *et al*., 1999).

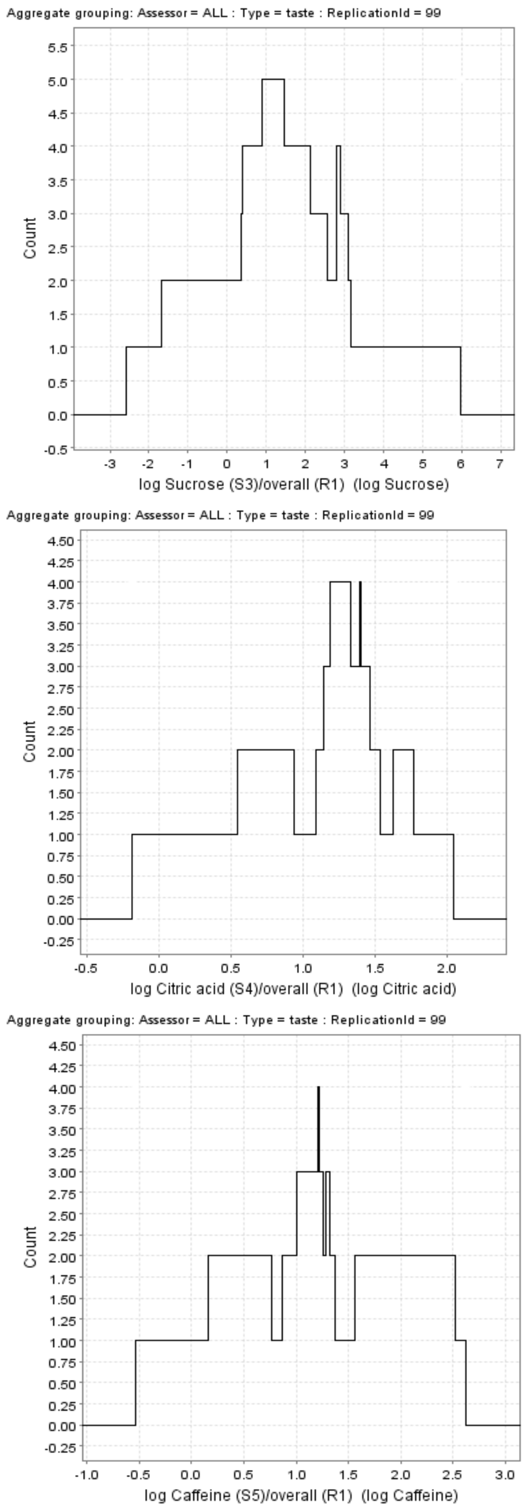
Quantity of MSG and Quality of a Food

It is in any case a fallacy to believe that the taste of glutamate makes a food more and more delicious as the anion's concentration increases without limit. As we have seen, for any familiar food or drink, each sensed constituent has a preference function which is peaked, not monotonic. Adding MSG does not automatically enhance flavour. The existing flavour is changed towards a generic savoury flavour. For the flavour to remain the same but become stronger, the balance among all its component tastes must be maintained by any additions (Booth & Freeman, 1993).

In other words, the learnt optimum strength of the taste based on quantity of MSG, or a similarly tasting mixture in a familiar food, is complemented by the quality of the taste. The same applies to any complex taste, and indeed to any odour, texture, colour pattern, shape etc. The quality of savoury taste, or more specifically of the taste of an inherently MSG-rich food such as ripe tomatoes, is the closeness to the correctly balanced mixture of tastes, as implicitly remembered by the eater.

Top quality of the taste of MSG in a familiar brand of salted tomato juice beverage can be measured as the balance of ideal points for each constituent of the matching mixture. The distribution of these most preferred (or most familiar) levels can be plotted in a histogram (as in Figure 7). The precision of each estimate is measured by Weber's fraction, with smaller fractions being better differential acuity. The resulting ideal ranges enable the plotting of frequency polygons without bins (Figure 11). The central tendency or modal frequency for each taste compound's most accepted level gives the concentration that is balanced with the group-wide most prevalent ideal point for each of the other varied taste compounds. The centre of the modal count gives similar proportions by weight among the three tastants (log 1.1 to log 1.3, i.e. 12.6 to 20). The median ideal points give proportions of sucrose 1.86 (with a very wide range), citric acid 1.43 and caffeine 0.92 log mg/100ml. The antilogarithms are 72:27:8.3 mg/100ml – approximately 8:3:1. These proportions by weight represent the balance of stimulation by the glutamate that dominates the taste of tomatoes.

Figure 11. Frequency polygons of individuals' ideal concentrations ($\log_{10}$ mg / 100 ml) of sucrose (top), citric acid (middle) and caffeine (bottom) in tomato juice beverage. Each count is a horizontal line from one half-discriminated fraction below the ideal point to one HDF above.



The Direct Route to Food Quality

The exact calculation of each taste's (and any other sensed component's) number of discrimination units away from the learnt standard mixture should enable better eating on all fronts. Foods and drinks can be redesigned to provide better support for the healthier habits of eating and drinking. The suppliers of foods can increase the wealth available by more economical production and marketing. We can all become a little happier by enjoying the best-tasting foods and drinks.

Olfactory Configurations in Ingestion

Good Balance Among Components

The theory of quality illustrated above for the complex savoury taste in one food can be expressed diagrammatically. The example plotted here is of the concentrations of two odour compounds forming part of a quaternary mixture that simulates the aroma of fresh strawberries (Figure 12). One constituent is maltol which has a sweetish smell, like a meringue. The other component in this two-dimensional illustration is ethyl acetoacetate. This compound by itself has a fruit-like aroma but the smell is not readily identifiable with any familiar fruit.

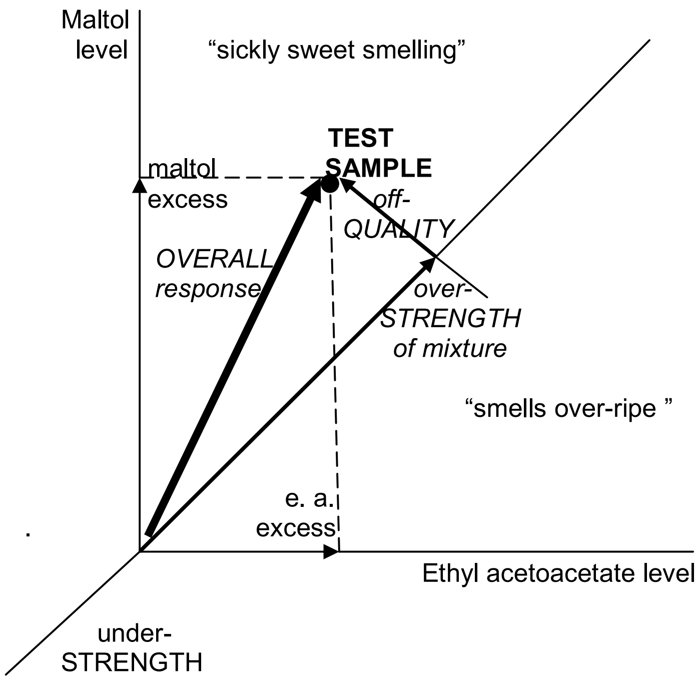
The strength of the strawberry aroma in a test sample is on the 45^{o} diagonal through the origin, which is each component's concentration at olfactory receptors in the strawberry norm in memory (Figure 12). The quality of the mixture, i.e. the balance of components, is the distance of the test sample along a perpendicular from the quantity diagonal. The off-aroma or lack of quality in the test sample is an excessively sweet smell in the example plotted. If the imbalance were in the opposite direction, the off-quality could be an over-ripe smell, or perhaps the hint of another fruit. These conceptualisations of defects in quality are objective in so far as an individual chooses words in accord with their successful use in the society speaking that language. That is, other appropriately acculturated assessors will agree with the verbal characterisation.

The discrimination-scaled measure of marketed good quality or the personally preferred mixture of two sensed constituents provides a theoretical basis for the pragmatic ratio used for example for the sugar and the cream in ice cream (Drewnowski & Greenwood, 1983; Drewnowski *et al.*, 1985).

The Aroma of Fresh Strawberries

Recognition of an odour is thought to be based on discrimination (Cain & Potts, 1996). Yet so far there has been only one implementation for olfaction of multisensory, multiconceptual cognition based on discrimination from a configural norm in memory (Booth & Freeman, 1993). This example was the aroma of a ripe de-hulled strawberry (Booth, Kendal-Read & Freeman, 2010b; Kendal-Reed & Booth, 1992a,b). The samples discriminated from that highly complex (and somewhat variable) natural mixture of volatiles were mixtures of just four odour compounds, each having its own assessor-named aroma note.

Figure 12. Strength/Quantity and Balance/Quality') for maltol ("sweet") and ethyl acetoacetate ("fruity"). Redrawn from Booth and Freeman, 1993, for two out of the four compounds in a mixture than can mimic the aroma of fresh strawberries.



Four recognisable notes dominate the smell of a strawberry. Since we learn to label smells by their sources, each note is named after another object or sort of material. For a fruit, smells from the plant world are favoured. The naming of an aroma as "sweet" probably arises from familiarity with caramelised sugary foods. "Green" (or "leafy") smell refers to the greenery on trees and bushes. "Fruity" is presumably a smell reminiscent of many species of fruit when ripe. The adjective "buttery" is a name learnt from the smell of that dairy product, or from volatiles added to spreads based on vegetable oil in order to give a flavour said to be like that of butter.

The remarkable fact exploited by the experiments illustrated next is that compounds having odours similar to each of these four sorts of material, when mixed in the appropriate proportions, have an aroma which is hard to distinguish from that of fresh strawberries. The multi-receptor profile of each compound (Polak, 1973; Malnic *et al*., 1999) may compensate to some degree for deficiencies in the profiles of one or more of the other compounds because each is similar, but not identical, to a major volatile in the headspace from strawberries (Ulrich *et al*., 1997). The fruity compound in the tested quaternary mixture is an ester but with a sharper note than the esters predominant in strawberries. Similarly, the leafy green smelling compound was a derivative of hexane (6-C) but not the compound dominant in strawberry itself. Maltol is formed when malts are roasted and it smells of caramelised sugar. Diacetyl occurs in butter at low enough levels to be characteristic of dairy fat, rather than blatantly of its animal origin.

Cognitive Analysis of Concentrations and Ratings

Ratings of the similarity of each test aroma to that of strawberries, and of the notes of each odorant in the mixture, need to be anchored on the smell of a real strawberry. Then the perceived distance from the configural norm of the level of each odorant in a sample mixture can be put on a scale in units of discrimination (Weber's fraction; the HDF). Since all the distances are in that same unit, they can be combined algebraically without any assumptions about how concentrations of different compounds relate to each other or to the rated intensities under the different concepts (Booth & Freeman, 1993).

There are two arithmetically simple possibilities (as stated above for taste mixtures). If two norm-zeroed discrimination functions are the same process (configured by learning about strawberries), then a sample's discrimination distances above or below the norm should add together, operating in the same cognitive dimension or over the same channel through the mind. If two of the odour compounds, the verbal concepts of notes, or the descriptions (concepts of compounds), are perceived as qualitatively different, then their norm-zeroed discriminations should be orthogonal, combining as the square root of the sum of the squares of the distances. As there were four odorants with a concept each, four-dimensional (4-d) models were tested. These calculations work if there are only three or two effective discriminations, or indeed just one. Similarly, the unidimensional (1-d) models had four components but the additive formula works even if fewer than four inputs were discriminated. Poor discrimination (a weak influence) merely places all the samples close to the norm.

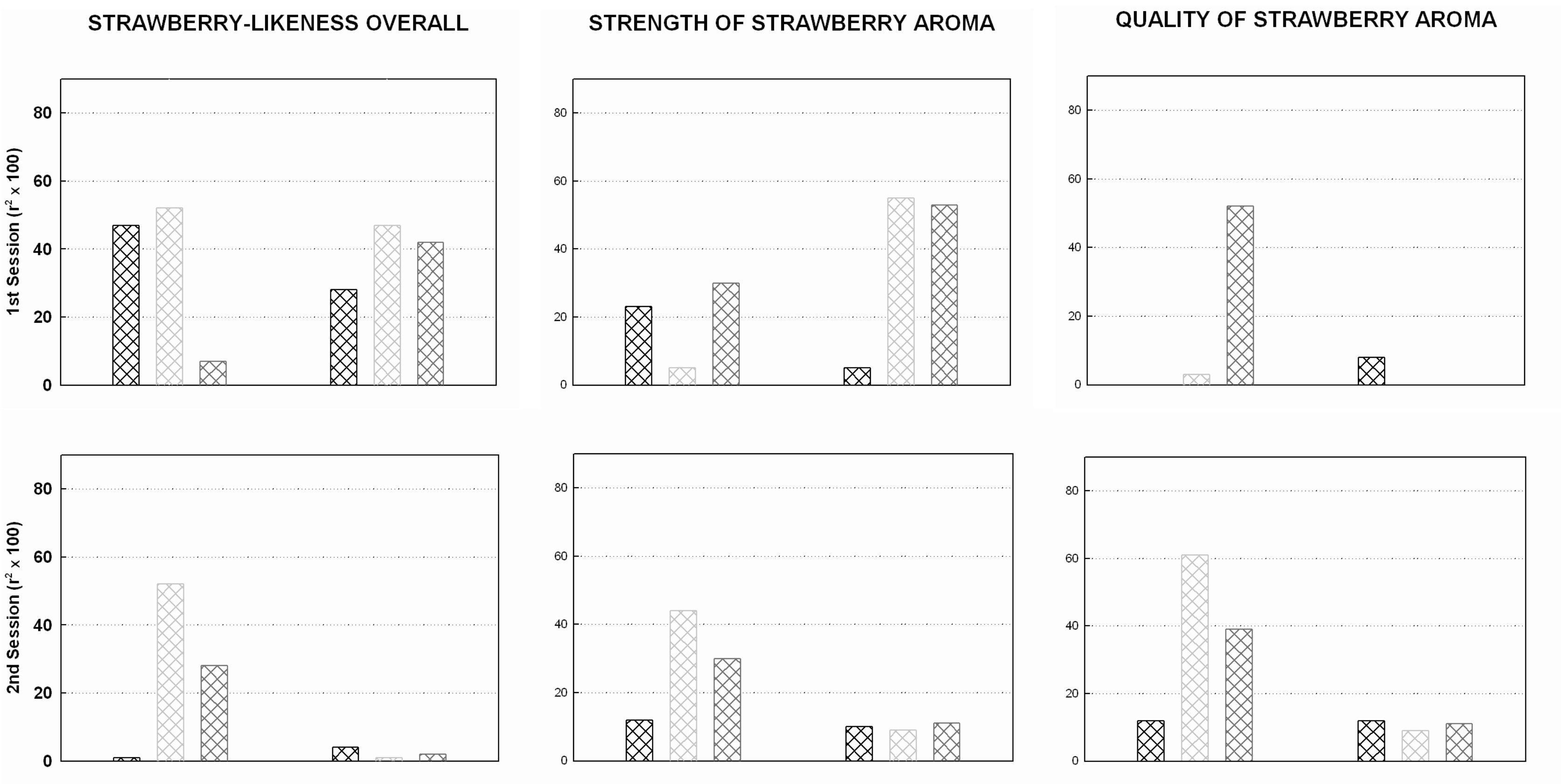
Regression from discrimination distance to rating of strawberriness (overall, strength or quality) was calculated for each sample for the odorant (an S), rating of a note (an R) and psychophysical function (an S/R). Those distances were summed into unidimensional integration (1-d) and combined by root sum of squares for multidimensdional integration (4-d). Linear regression from distances to strawberriness scores gave the variance accounted for by each model (r^2; vertical axes in Figure 13).

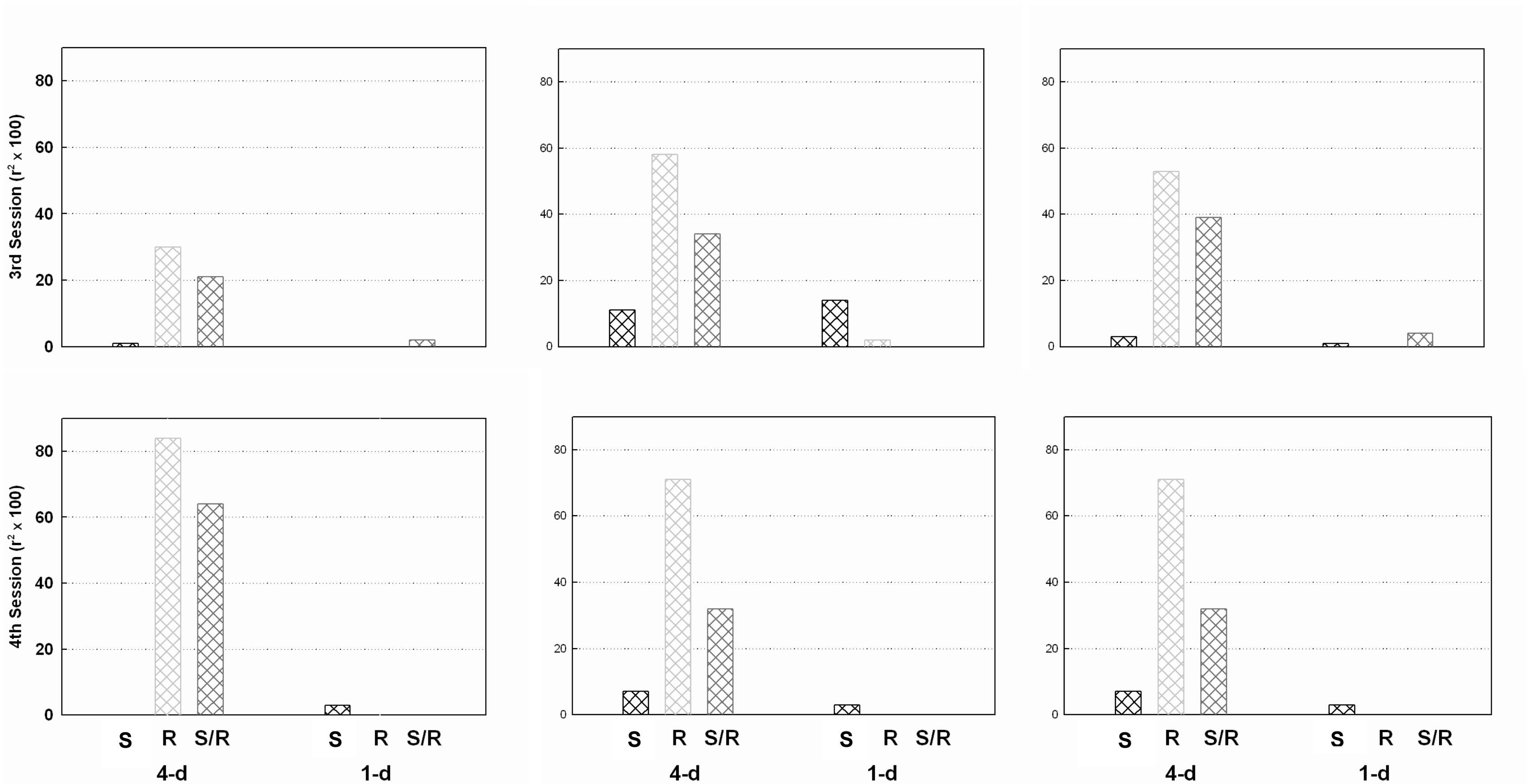
Analytical and Configured Norms

The assessor whose olfactory processing is summarised here assessed overall strawberriness of the mixtures (left-hand column of Figure 13) by use of the analytical concepts of sweet, leafy, fruity and creamy throughout the four sessions - that is, four-dimensional processing, using the concepts alone (R) or in descriptions of the odorants (S/R). Nevertheless, 4-d stimulation (S) processing and 1-d conceptual (R) and descriptive (S/R) processing were almost equally as well evidenced in the first session. The analytical concepts rapidly gained in influence on the recognition of strawberry aroma in the tested mixtures, with the other processes dropping out, leaving solely the 4-d conceptual and descriptive processing in the fourth session (bottom left panel of Figure 13). This finding is consistent with the view that practice with quantitative descriptive analysis interferes with configural perception, as might mediated by immediate judgments of preference or familiarity (Barkat, Le Berre, Coureaud *et al*., 2012). Another factor that could have weakened the configuring is that at least two of the four analytical concepts -- sweet and fruity -- are likely to have been similar to the integrative concept of strawberry (Derby, Hutson, Livermore & Lynn, 1996; Kay & Stopfer, 2006).

End of Portrait

Figure 13. Cognitive processes integrating concentrations of four odour compounds into "strawberry" aroma. Each row of graphs comes from one session, from the first (top) to the fourth. Each mixture was rated first for overall similarity to the aroma of the fresh strawberry presented in the same way just before the mixture. Then the strength of the mixture's strawberry aroma was rated and finally how the good the mixture was as the aroma of strawberry (see Figure 12). Both separate processing of up to four components (4-d) was calculated and configuring into a single process (1-d). Discriminative predictors were calculated from the concentrations of stimuli directly (S), from the concept of strength and/or quality (R) or description of the stimulus in terms of that concept (S/R). (Case B in Booth *et al*., 2010b). *Figure continues on next page. Axis labels only on bottom row and left-hand column of panels.*





End of Landscape

Assessment of the strength of the strawberry aroma and the quality of the balance among odorants showed complementary learning. Judgments of strength were initially more configural (top middle panel, Figure 13). That is, the use of fresh strawberry as a standard set up a distinct holistic similarity among the concepts and descriptions. Nevertheless, as overall judgments became more analytical, so strength was decided more by separate concepts. Unsurprisingly the judgments of balance never used configural processing (right-hand column in Figure 13). Analytical description dominated quality initially (top right panel, Figure 13) but conceptualisation made an increasing contribution, resulting in a very similar pattern of processing of all three judgments by the fourth session (bottom right panel, Figure 13).

Both strength and quality judgments were distinguished from overall judgments by use of both analytical and configural processing of the olfactory stimulation (S processes). The contribution of direct stimulatory processing remained very small throughout, starting largest for strength (top middle panel, Figure 13). Yet it was consistent throughout later sessions of both analytically and holistically decided judgments of strength and quality, while never appearing in overall strawberriness.

The above results from one experiment with one person are of course merely illustrative. Nevertheless, they established the feasibility of person-by-person and situation-by-situation characterisation of mediating cognitive processes in mixtures of odour compounds that come close enough to simulating a familiar aroma. Clearly the ratios of concentrations presented are critical. If any one of them departs substantial from balance, the integrative and analytical tasks relative to the standard in memory may become impossible.

In addition, this approach provides a single solution for two major quantitative issues in olfaction (Booth, 1995; Booth & Freeman, 1993). One issue is the fundamental principles for measuring the quality of an odour (Wise, Olsson & Cain, 2000). The traditional ‘difference tests’ are not fully objective unless each sample’s number of discriminations from norm is estimated (Booth, 1995; Booth & Freeman 1993). They are also far more laborious than is needed to detect differences, let alone to optimise quality. The other issue is how to specify the proportions of components in a mixture that can be configured into a familiar aroma (Jinks & Laing, 2001; Le Berre *et al*., 2008) or taste, texture, colour, etc. This too is achieved rapidly and objectively by scaling discrimination distances from norm, as illustrated here and elsewhere (Booth & Conner, 1991; Booth & Freeman, 1993; Booth *et al*., 1989, 2003a,b,c, 2010a,b, 2011a,b,c). Furthermore, this solution to both problems is general to any sensory modality and indeed also to purely verbal or pictorial influences on preference.

Flavour

An obvious extension of this early work on tastants and on odorants was to learnt configural norms of taste and odour in combination. Rated satiety to olfactory and visceral sensing has met the criterion for learnt configuring (Booth, 2013; Booth *et al*., 1994). Configural integration of odour with taste occurs with sweetness at least (Prescott & Murphy, 2009). Norm-zeroed discrimination analysis of performance before and after learning could advance associative theory in ways that categorical stimuli cannot do because they do not have intradimensional generalisation gradients (Pearce, 1994, 2002).

Particular levels of tastes and aromas (and colours) can be configured into the unique flavour of a food or drink. The collapse of New Coke, arguably the worst product development mistake ever made, was primarily excessive sweetness caused by poor methods of measuring ideal sweetness (Booth & Shepherd, 1988), although the introduction of a new flavouring also played a part. Familiarity with a brand of cola (perhaps almost from weaning!) establishes a highly precise memory of its taste and smell, as well as cooled temperature, level of fizz and colouring.

Configuring of Taste and Odour

It has recently begun to be recognised that the tastes and odours in familiar flavours do not add or multiply together (or suppress each other) in concentrations or in ratings but interact "cognitively" (Davidson *et al*., 1999). This fact invalidates longstanding claims to intensification of taste by odour or vice versa (Auvray & Spence, 2008). However, discrimination scaled data on configuring of taste and odour mixtures have yet to be published. The pilot analyses below indicate that the cognitively realistic approach could start to clear up the mess caused by inattention to the mental mechanisms of integration of inputs into ingestive output.

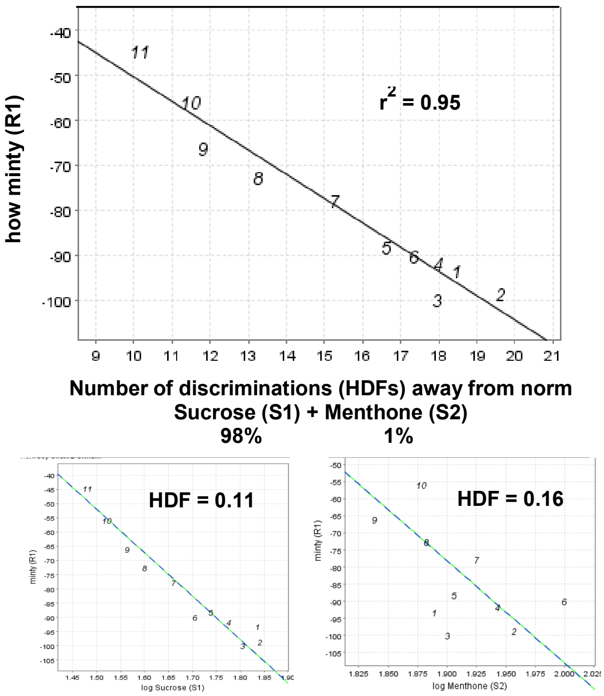
The concentrations in air of the volatile compounds in the peppermint flavouring of chewing gum were measured continuously in the breath in the nostrils that flows outwards swallow by swallow. Menthone is a major contributor to the minty smell and so was taken as an indicator of concentrations across the profile of compounds measured by gas chromatography coupled with mass spectrometry. Sucrose concentration in saliva was measured every few seconds by the same technology (Davidson *et al*., 1999).

The sugar in a piece of gum begins to dissolve out quickly from the start of chewing. The gum (famously) becomes depleted within a few minutes. The steady decline in salivary sucrose concentration contrast with a rise in menthone concentration is air in the mouth that goes into the nose up the back of the throat. This takes a minute or two to reach a peak and then declines somewhat more slowly. Hence there is a set of menthone levels on either side of the peak that are essentially uncorrelated with the monotonic declining in sucrose levels. Rapidly repeated quantitative judgments of how "minty" the flavour currently is were used to construct a time-intensity profile.

Hence the separate effects of sucrose and menthone stimulus levels on "minty" judgments can be measured. The various possible cognitive interactions between "minty"/[sucrose] and "minty"/[menthone] can be calculated to determine which of those hypotheses accounts for the greatest proportion of the variance in how "minty" the gum is said to be (Booth & Freeman, 1993) at any moment around the time that menthone levels in the nares reach their maximum.

Data for three sessions from different people are presented here. They illustrate the variety of cognitive processes that combine gustatory and olfactory information into the information conveyed by each individual's use in this context of society's objective verbal concept of a flavour. Sucrose and menthone were configured into "minty" in two of the three sessions but in very different ways. In one person (Figure 14), menthone provided the merest hint of a flavour to the sucrose being dissolved out of the coating of the tablet of gum. Yet in another set of data

Figure 14. Best supported hypothesis of cognitive processing of sucrose taste and menthone aroma in intensity of "minty" around the peak release of menthone during chewing of a tablet of gum (upper graph). Menthone and sucrose concentrations were configured into a single determinant of "minty" but menthone made only a very slight contribution, perhaps because of a less powerful effect, as measured by the half-discriminated fraction (lower pair of graphs). Data point numbers: sequence of concentrations delivered by chewing. The raw data from GC-MS in this and the following two Figures were kindly provided by Bob Davidson and Andy Taylor, University of Nottingham (cp. Davidson *et al*., 200x).



(Figure 15), menthone dominated the "minty" intensity while sucrose made a minor contribution, while the participant in Figure 16 responded the other way round, with menthone in a minor role. Nevertheless, all three analyses were dominated by configural processing, with signals from the two distinct modalities being transmitted over a single channel to the intensity of minty flavour. There was also some evidence than menthone was not a perfect match to the norm for "minty". As well as the emergent 'third stimulus' of configured menthone and sucrose, another aspect of menthone acted on its own (Figure 15). This may have been the parts of the olfactory receptor stimulation profile from menthone that most closely matched that of the whole spearmint aroma.

Figure 15. Best supported hypothesis of cognitive processing of “minty” intensity during peak release of menthone from a chewed tablet of gum in an assessor who configured sucrose and menthone concentrations into an integration flavour dominated by menthone and also had a separate small contribution from menthone alone. Nevertheless, both sucrose and menthone had a very weak influence on “minty” and their concentrations were all a long way above ideal (lower two graphs). Data point numbers: sequence of concentrations delivered by chewing.

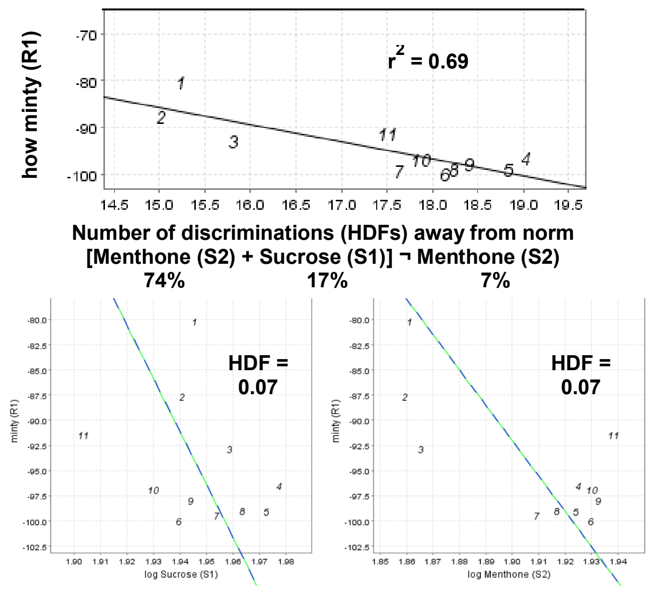
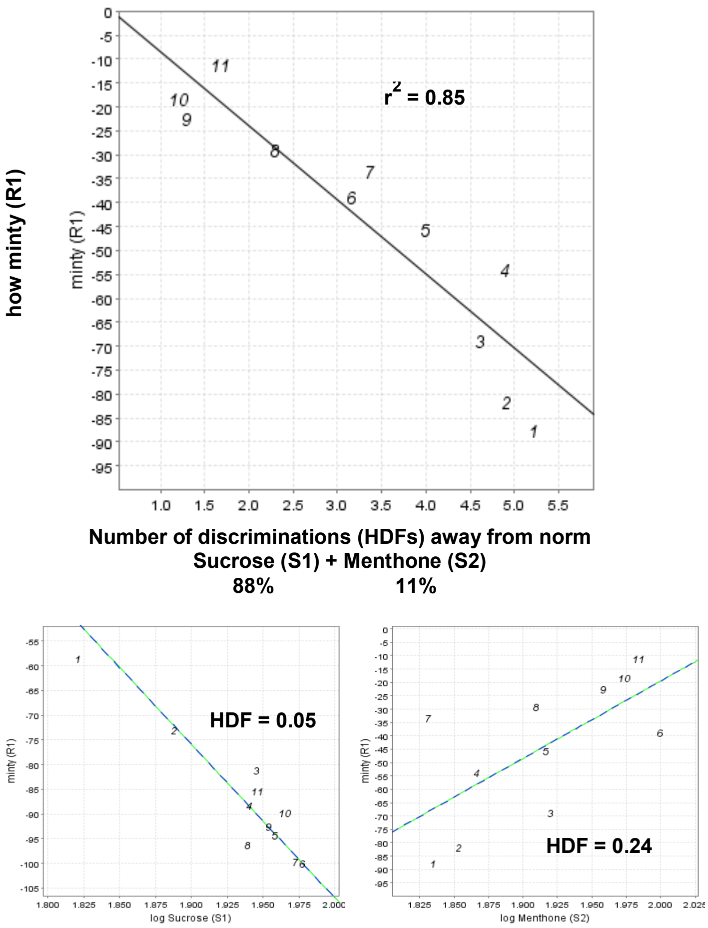


Figure 16. Best supported hypothesis of cognitive processing of "minty" intensity in an assessor who configured sucrose and menthone concentrations into "minty". This integrated flavour was mostly the taste of sucrose but with a definite aroma of menthone. The lower pair of graphs show that levels of sucrose were very well discriminated (Weber fraction of 5%) but menthone levels not so well. At this peak of release of menthone into the nares, all the sucrose concentrations on the tongue were above ideal for "minty" in gum while all the concentrations of menthone in the nares were below ideal – albeit including levels very close to ideal in both cases.



An alternative interpretation is that “minty” was not used to describe the volatiles of the spearmint flavouring in chewing gum, albeit cognitively modulated in strength by the taste of sucrose. It may have been used as a name for the candy imitated by gum (until it has lost its flavour). In that case, the norm in the memory that the word ‘mint’ invoked would be the flavour of peppermint candy, which is overwhelmingly sweet. The normal balance of sweetness and peppermint aroma while sucking the candy was read from memory into the mixture of olfactory and gustatory stimuli presented as the volatilisation of menthone from the chewing gum reached its peak. These of course are major practical issues for formulators of chewing gum for consumers’ perceptions of quality. As in other areas of application of science, the most effective approach may be measurement of what each user of the product is doing, rather than statistical modelling of numbers collected from experts or customers without considered the mechanisms that generate the numbers.

Flavours of Cuisines, not Nutrients

It was well argued long ago that flavours are not biologically determined but a cultural inheritance (E. Rozin, 1973). Yet it is still claimed that sweetness signals calories, saltiness signals sodium, fats have a taste, protein would not be recognised without a glutamate receptor, and aromas give emotional meaning to foods ahead of the material acquiring a culinary role in an individual’s life. In fact, since the rise of agriculture, most of the energy in the human diet has come from grain starch. Hunter-gatherer groups are most unlikely to have been rescued from extinction by honey from wild bees’ nests. The ripening of fruit merely makes its energy content more digestible. Instead it has been suggested that any selective pressure on the human sweet receptor could have arisen from its sensitivity to the free amino acids in milk countering bitterness in immunity promoting glycopeptides.

Also, as we saw at the start of this chapter, human adult’s appetite for sweetness, as for every other characteristic of a food, is learnt for each level (sometimes quite low) that is specific to a particular food habitually eaten (Conner *et al*., 1986, 1988c). Such learning of preferences may be facilitated by hunger or a long established norm of the hunger-reducing role of the flavoured material (Irvine, Brunstrom, Gee & Rogers, 2013). The basic mechanism of glucose-conditioned sensory preference in naive rats can be configured with an internal state but that signal can be from filling of the digestive tract with non-nutritive fluid, not necessarily a carbohydrate specific deficit (Gibson & Booth, 1989).

Similarly, as we saw above, there is no solid evidence for an innate appetite for sodium salts in human beings. Salt-deficient people may choose saltier foods (e.g., Leshem *et al*., 2008) but that could be a learnt appetite. Some selections of foods from the available cuisine may do better than others in rapidly repairing all the physiological components of a sodium deficit. That configural memory could produce the shift in sensory preferences when the signalled need for sodium recurs (cp. Booth, 2013).

Long-term effects of taste on nutrition

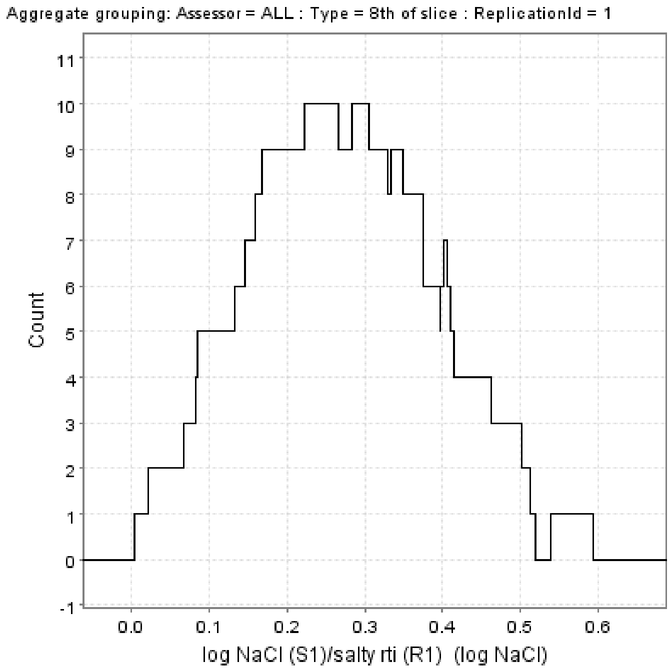
Salt and Strokes

Long term problems with too much taste are less obvious and may be hard to solve. For instance, we all need a little salt each day. Yet that amount of sodium ions is far less than we consume from foods that we eat in quantity such as bread, pies and biscuits. We do not think of pastry as salty food but a little salt is part of the character of a pie's crust and casing, and so the tradition continues of adding some to the dough. We may have a seriously salty item like a bag of potato crisps or a drink of tomato juice, or we may shake salt over the food on the plate. The result is that the body has to cope with a rush of salt during digestion of the meal. To keep sodium levels normal, water gets pushed into the blood and its pressure goes up. That stretches the muscles in the walls of arteries and so they get stronger. The result may be a persistently high pressure in the circulation, which is a danger to weaker blood vessels like those in the brain. Hence there is an international problem with strokes to which lifetimes of salt intake have contributed.

How can we reduce the salt content of meals when eaters demand the levels of salt that they are accustomed to? The simplest answer in principle is to reduce the level in each food one step at a time which is barely noticeable. Consumers who are interested can see what is happening in the information on the pack about nutrient contents. The changes should not be advertised as 'healthier' even though there is evidence to support that claim, because decades of poorly designed changes in sensed characteristics in the name of health has created the stereotype that healthy tastes bad and good tasting food is unhealthy (Raghunathan, Naylor & Hoyer, 2006).).

There is so far no substitute for sodium chloride that gives its clean salty taste, even if it were save and inexpensive enough for wide use. Substitutes (and amplifiers of the salty taste) found thus far have unfamiliar and therefore at least initially unpleasant side tastes. Hence a substitute might work only in foods that already have other strong tastes that mask its side taste. Bland foods eaten in large amounts, such as bread, are therefore a serious problem for the search for substitutes. If there is not enough salt in bread to stop sodium ion levels in saliva being reduced, the unpleasant taste of distilled water can emerge and the bread tastes like cardboard. Nevertheless traditional levels are far above this minimum. Some people on a medically prescribed low-salt diet come to prefer a lower concentration of salt in a test food (Pangborn & Pecore, 1982). Hence if the salt level in bread were lowered by a barely detectable amount and consumers become familiar with the reduced level, they are all likely to come to prefer that level. After that, the level can be further lowered by a similar proportion. Such a strategy requires accurate data on each consumer's most preferred level of salt in the food product to be adjusted. Individuals' ideal points for salt in plain bread can be determined accurately from small amounts of data if the cognitive mechanisms of sensing are correctly exploited (Booth *et al*., 1983; Conner *et al*., 1988a). The frequency profile of ideal points indicates that there could be no impact on sales from a reduction by 10-15% (Figure 17). The most sensitive assessor who tolerated salt levels up to 2% would not have changed preference with a reduction of 10-15%. The next lowest tolerance was for a reduction of about 20%. A few assessors found the saltiness of the plain bread very salient (narrow HDFs) and had ideal points well above 2%. Pieces of bread without spread were tested, however, whereas these people would presumably have put a salty covering on their bread.

Figure 17. Directly observed prevalences of ideal ranges for salt in bread (N = 15). Each horizontal line begins at an assessor's ideal point minus one Weber fraction (HDF) and ends at an ideal point plus one HDF, excluding assessors with very wide HDFs. In these calculations, the determinant of preference was modelled as the cognitive process of describing sodium chloride as being "salty" in taste. rti: relative to ideal. log NaCl: $\log_{10}$ of grams of sodium chloride in 100 g of bread. (Reanalysis of data presented in Booth, Thompson & Shahedian, 1983.)



Lowering the salt content of bread happens to reduce costs in yeast as well as salt. Hence major bakers in the UK were able to make year-on-year reductions in salt in the most popular brands of bread during the 1990s. The governmental regulatory agency then took advantage of this lead to persuade producers of other foods to reduce salt levels. Unfortunately, however, progress is limited in the UK and other countries by failure to correct standard practice in sensory evaluation of consumer preferences. First, the set of food samples has to be designed to remove upward biases created by presenting unfamiliarly high concentrations (Conner, Land & Booth, 1987; Riskey, Parducci, Beauchamp, 1979). Secondly, the rating and analyses of the data must measure each person's ideal point ("just right"), rather than degrading the data to a range that is broadly acceptable ("just about right") and has indeterminate boundaries with categories of unacceptably high and low (Booth & Conner, 2009).

Sugar and Teeth

Sweetness has been posed as a problem for morality as well as for medicine (Rozin, 1986). The only proven problem though is from leaving sugar repeatedly on the teeth at intervals of less than an hour. It is irrelevant how much sugar was eaten. Bacteria that are always in the mouth make acid from whatever little sugar is left. That softens the enamel. If it has no time to harden, rot sets in. A low level of fluoride slows the softening but plainly it is wise to wait at least an hour or two before having something else sugary after eating chocolate or cake, and especially candy that sticks on the teeth. Health campaigners would help more by a focus on that risky pattern of actions, instead of letting the scene be stolen by fulminations against sugar regardless of use.

If there is a connection between sweetness and a child's obesity, it is not sugar but a habit of eating lots of sugary food. Lots of starchy food is just as fattening, and fatty foods even more so. A growing child needs meals that are large and varied enough to go through to the next meal, four or five times a day when the child concentrates just on eating and drinking and is given no more first course than is eaten up and leaves space for a little mildly tasting dessert. Foods supplied to children should not exploit the inborn attraction to sweet stuff.

Anyone who fears loss of control to intense pleasure should relax about sugar. The innate reflex to strong sweetness by itself has been suppressed by all the learning to like the moderate level of sweetness specific to each ordinary food and drink.

Conclusions

Mechanisms versus Tests

The state of the art remains reliant on group averaging of numbers taken from tests of meal sizes (weight of each food, total energy content, etc.), sensory descriptive analysis, ratings of appetite ("how much will you eat then?", "how full are you now?"), modality-specified preferences (liking for taste, aroma, colour etc.), and so on, with or without statistical analyses that allows for the redundancies among supposedly different measures. All of these approaches fail to address the basic scientific question: which stimuli actually control each (non-redundant) response?

It is logically impossible to start answering this question until potential influences on a response are measured, as well as the test response itself, whatever influence some investigators assume that it reflects. Those measurements of stimuli have to show that their levels vary independently of each other across the tested samples, because the effects caused by simultaneous variations cannot be separated, again as a matter of logic.

Chemosensory Influences on Nutrition

This chapter should have made crystal clear why it is fundamentally misconceived to try to measure the effects of sweetness on meal size, insulin resistance or market share, of concentration of glutamate or added aroma on appetite in older people, or of genetic sensitivity to bitterness on food choices or rated preferences. Measurements of blood chemistry relate very poorly related to usual daily intake of the relevant nutrients. The chances of sensed chemical constituents of foods bearing a clear relation to nutritional health must be even more remote.

A single mechanism that varies the choice of each mouthful cannot be expected to bear on the intake of any nutrient. Even in the apparently most straightforward instance, the ideal points for salt in various foods bear little relation to daily sodium intake (Shepherd, 1988). As an absolute minimum, each individual's ideal point for the taste or aroma under investigation needs to be measured for each key food in a regular pattern of eating that has been shown to have the nutritional effect of interest.

Often the potentially relevant foods or eating habits have yet to be measured in a way that identifies a mechanism for its effect. For example, the basic facts about fattening habits remain to be determined. If an individual maintains a change in frequency of a communally identified eating habit, how big is the step change in weight caused by that alteration in rate of energy intake (Hall, Sacks, Chandramohan *et al*., 2011)? When an eating habit has been shown to be effective, then the question arises which foods and drinks dominate that habit (Booth & Booth, 2011; Booth & Nouwen, 2011; Laguna-Camacho & Booth, under review). At that stage, measurement of sensory and other influences on choice can be used for scientific investigation of nutritional consequences.

There are feasible ways forward to understanding the roles of taste and smell in nutrition. Indeed, they have been available for several decades. As in genomics, neuroscience, individual development or qualitative research, there is no alternative, even in the medium term, to publishing reports that relate the observations to the relevant known causal processes.

References

Auvray, M., & Spence, C. (2008). The multisensory perception of flavour. *Consciousness and Cognition* 17, 1016-1031.

Baker, B.J., Booth, D.A., Duggan, J.P., & Gibson, E.L. (1987). Protein appetite demonstrated: learned specificity of protein-cue preference to protein need in adult rats. *Nutrition Research* 7, 481-487.

Barkat, S., Le Berre, E., Coureaud, G., Sicard, G., & Thomas-Danguin, T. (2012). Perceptual blending in odor mixtures depends on the nature of odorants and human olfactory expertise. *Chemical Senses*37, 159-166.

Bartoshuk, L.M., Duffy, V.B., & Miller, I.J. (1994). PTC/PROP tasting: anatomy, psychophysics and sex effects. *Physiology and Behavior* 56, 1165-1171.

Beauchamp, G.K., & Moran, M. (1982). Dietary experience and sweet taste preference in human infants. *Appetite* 3, 139-152.

Behrens, M., Foerster, S., Staehler, F., Raguse, J.D,, & Meyerhof, W. (2007). Gustatory expression pattern of the human TAS2R bitter receptor gene family reveals a heterogenous population of bitter responsive taste receptor cells. *Journal of Neuroscience* 27,12630-12640.

Beidler, L.M. (1954). A theory of taste stimulation. *Journal of General Physiology* 38, 133-139.

Berridge, K.C., & Grill, H.J. (1983). Alternating ingestive and aversive consummatory responses suggest a two-dimensional analysis of palatability in rats. *Behavioral Neuroscience* 97, 563-573.

Berridge, K.C., & Robinson, T.E. (2003). Parsing reward. *Trends in Neuroscience* 26, 507-513.

Berridge, K.C., Venier, I.L., & Robinson, T.E. (1989). Taste reactivity analysis of 6-hydroxydopamine-induced aphagia: implications for arousal and anhedonia hypotheses of dopamine function. *Behavioral Neuroscience* 103, 36-45.

Blundell, J.E., & Hill, A.J. (1986). Paradoxical effects of an intense sweetener (aspartame) on appetite. *Lancet* (8489), 1092-1093.

Booth, D.A. (1972a). Taste reactivity in satiated, ready to eat and starved rats. *Physiology and Behavior* 8, 901-908.

Booth, D.A. (1972b). Conditioned satiety in the rat. *Journal of Comparative and Physiological Psychology* 81, 457-471.

Booth, D.A. (1974). Acquired sensory preferences for protein in diabetic and normal rats. *Physiological Psychology* 2, 344-348.

Booth, D.A. (1976). Approaches to feeding control. In T. Silverstone (Ed.), *Appetite and food intake*, pp. 417-478. West Berlin: Abakon Verlagsgesellschaft / Dahlem Konferenzen. http://epapers.bham.ac.uk

Booth, D.A. (1979). Metabolism and the control of feeding in man and animals. In K. Brown & S.J. Cooper (Eds.), *Chemical influences on behaviour*, pp. 79-134. London: Academic Press.

Booth, D.A. (1985). Food-conditioned eating preferences and aversions with interoceptive elements: conditioned appetites and satieties. *Annals of the New York Academy of Sciences* 443, 22-37.

Booth, D.A. (1988). Mechanisms from models - actual effects from real life: the zero-calorie drink-break option. *Appetite* 11, Supplement, 94-102.

Booth, D.A. (1990). How not to think about immediate dietary and postingestional influences on appetites and satieties. *Appetite* 14, 171-179.

Booth, D.A. (1991). Learned ingestive motivation and the pleasures of the palate. In R.C. Bolles (Ed.), *The hedonics of taste*, pp. 29-58. Hillsdale NJ: Erlbaum.
Booth, D.A. (1994). *Psychology of nutrition*. Hove & New York: Psychology Press.
Booth, D.A. (1995). Cognitive processes in odorant mixture assessment. *Chemical Senses* 20, 639-643.
Booth, D.A. (2005). Perceiving the texture of a food: biomechanical and cognitive mechanisms and their measurement. In E. Dickinson (Ed.), *Food colloids: interactions, microstructure and processing*, pp. 339-355. Cambridge: Royal Society of Chemistry.
Booth, D.A. (2008). Physiological regulation through learnt control of appetites by contingencies among signals from external and internal environments. *Appetite* 51, 433-441.
Booth, D.A. (2009a). Learnt reduction in the size of a meal. Measurement of the sensory-gastric inhibition from conditioned satiety. *Appetite* 52, 745-749.
Booth, D.A. (2009b). Lines, dashed lines and "scale" ex-tricks. Objective measurements of appetite *versus* subjective tests of intake. *Appetite* 53, 434-437.
Booth, D.A. (2013). Configuring of extero- and interoceptive senses in actions on food. *Multisensory Research* 26, 123-142.
Booth, D.A. (under review). How a mind works. II. A fundamental theory of the individual's actions, perceptions, feelings and thoughts. Submitted on 2 September 2013.
Booth, D.A., & Baker, B.J. (1990). dl-Fenfluramine challenge to nutrient-specific textural preference conditioned by concurrent presentation of two diets. *Behavioral Neuroscience* 104, 226-229.
Booth, D.A. & Booth, P. (2011). Targeting cultural changes supportive of the healthiest lifestyle patterns. A biosocial evidence-base for prevention of obesity. *Appetite* 56, 210-221.
Booth, D.A., & Conner, M.T. (1991). Characterisation and measurement of influences on food acceptability by analysis of choice differences: theory and practice. *Food Quality & Preference* 2, 75-85.
Booth, D.A., & Conner, M.T. (2009). Salt in bread. [Letter to the Editor] *Journal of Food Science* 74(3), vii-viii.
Booth, D.A., & Davis, J.D. (1973). Gastrointestinal factors in the acquisition of oral sensory control of satiation. *Physiology and Behavior* 11, 23-29.
Booth, D.A., & Freeman, R.P.J. (1993). Discriminative feature integration by individuals. *Acta Psychologica* 84, 1-16.
Booth, D.A., & Miller, N.E. (1969). Lateral hypothalamus mediated effects of a food signal on blood glucose concentration. *Physiology and Behavior* 4, 1003-1009.
Booth, D.A., & Nouwen, A. (2011). Weight is controlled by eating patterns, not by foods or drugs. Reply to comments on "Satiety -- no way to slim." *Appetite* 57, 784-790.
Booth, D.A., & Shepherd, R. (1988). Sensory influences on food acceptance - the neglected approach to nutrition promotion. *BNF Nutrition Bulletin* 13(1), 39-54.
Booth, D.A., & Simson, P.C. (1971). Food preferences acquired by association with variations in amino acid nutrition. *Quarterly Journal of Experimental Psychology* 23, 135-145.
Booth, D.A., Blair, A.J., Lewis, V.J., & Baek, S.H. (2004). Patterns of eating and movement that best maintain reduction in overweight. *Appetite* 43, 277-283.
Booth, D.A., Campbell, A.T., & Chase, A. (1970). Temporal bounds of postingestive glucose-induced satiety in man. *Nature* 228, 1104-1105.
Booth, D.A., Chase, A., & Campbell, A.T. (1970). Relative effectiveness of protein in the late stages of appetite suppression in man. *Physiology and Behavior* 5, 1299-1302.

Booth, D.A., Conner, M.T., & Gibson, E.L. (1989). Measurement of food perception, food preference, and nutrient selection. *Annals of the New York Academy of Sciences* 561, 226-242.

Booth, D.A., Earl, T., & Mobini, S. (2003a). Perceptual channels for the texture of a food. *Appetite* 40, 69-76.

Booth, D.A., Freeman, R.P.J., Konle, M., Wainwright, C.J., & Sharpe, O. (2011a). Perception as interacting psychophysical functions. Could the configuring of features replace a specialised receptor? *Perception* 40, 509-529.

Booth, D.A., Gibson, E.L., Toase, A.-M. & Freeman, R.P.J. (1994). Small objects of desire: the recognition of foods and drinks and its neural mechanisms. In C.R. Legg & D.A. Booth (Eds.) *Appetite: neural and behavioural bases*, pp. 98-126. Oxford: Oxford University Press.

Booth, D.A., Higgs, S., Schneider, J., & Klinkenberg, I. (2010a). Learned liking versus inborn delight. Can sweetness give sensual pleasure or is it just motivating? *Psychological Science* 21, 1656-1663.

Booth, D.A., Jarvandi, S., & Thibault, L. (2012). Food after deprivation rewards the earlier eating. *Appetite* 59, 790-795.

Booth, D.A., Kendal-Reed, M.S., & Freeman, R.P.J. (2010b). A strawberry by any other name would smell as sweet, green, fruity and buttery. Multisensory cognition of a food aroma. *Appetite* 55, 738-741.

Booth, D.A., Lee, M., & McAleavey, C. (1976). Acquired sensory control of satiation in man. *British Journal of Psychology* 67, 137-147.

Booth, D.A., Konle, M., & Sharpe, O. (2008). Taste of savoury foods does not need a fifth receptor type. (Abstract at SSIB, Paris) *Appetite* 51, 355.

Booth, D.A., Lovett, D., & McSherry, G.M. (1972). Postingestive modulation of the sweetness preference gradient in the rat. *Journal of Comparative and Physiological Psychology* 78, 485-512.

Booth, D.A., Mather, P., & Fuller, J. (1982). Starch content of ordinary foods associatively conditions human appetite and satiation, indexed by intake and eating pleasantness of starch-paired flavours. *Appetite* 3, 163-184.

Booth, D.A., Mobini, S., Earl, T., & Wainwright, C.J. (2003b). Consumer-specified instrumental quality of short-dough cookie texture using penetrometry and break force. *Journal of Food Science: Sensory and Nutritive Qualities of Food* 68, 382-387.

Booth, D.A., Mobini, S., Earl, T., & Wainwright, C.J. (2003c). Market-optimum instrumental values from individual consumers' discriminations of standard sensory quality of the texture of short-dough biscuits. *Journal of Food Quality* 26, 425-439.

Booth, D.A., O'Leary, G., Li, L., & Higgs, S. (2011c). Aversive viscerally referred states and thirst accompanying the sating of hunger motivation by rapid digestion of glucosaccharides. *Physiology and Behavior* 102, 373-381.

Booth, D.A., Sharpe, O., & Conner, M.T. (2011d). Differential gustatory sensitivity to caffeine in normal use points to supertasters, tasters and non-tasters. *Chemosensory Perception* 4, 154-169.

Booth, D.A., Sharpe, O., Freeman, R.P.J., & Conner, M.T. (2011e). Insight into sight, touch, taste and smell by multiple discriminations from norm. *Seeing and Perceiving* 24, 485-511, 639.

Booth, D.A., Thompson, A.L., & Shahedian, B. (1983). A robust, brief measure of an individual's most preferred level of salt in an ordinary foodstuff. *Appetite* 4, 301-312.
Bowman, S.J., Booth, D.A., Platts, R.G., & the UK Sjögren's Interest Group (2004). Measurement of fatigue and discomfort in primary Sjogren's syndrome using a new questionnaire tool. *Rheumatology* 43, 758-764.
Breslin, P.A.S., Beauchamp, G.K., & Pugh, E.N. (1996). Monogeusia for fructose, glucose, sucrose and maltose. *Perception and Psychophysics* 58, 327-341.
Breslin, P.A.S., Kemp, S., & Beauchamp, G.K. (1994). Single sweetness signal. *Nature* 369, 447-448.
Breslin, P.A.S., Gilmore, M.M., Beauchamp, G.K., & Green, B.G. (1993). Psychophysical evidence that oral astringency is a tactile sensation. *Chemical Senses* 18, 405-417.
Cabanac, M. (1971). Physiological role of pleasure. *Science* 173, 1103-1107.
Cabanac, M. (1979). Sensory pleasure. *Quarterly Review of Biology* 54, 1-29.
Cabanac, M., & Duclaux, R. (1970a). Specificity of internal signals in producing satiety for taste stimuli. *Nature* 227**,** 966-967.
Cabanac, M., & Duclaux, R. (1970b). Obesity: absence of satiety aversion to sucrose. *Science* 168, 496-497.
Cabanac, M., Minaire, Y, & Adair, E.R. (1968). Influence of internal factors on the pleasantness of a gustative sweet sensation. *Communications in Behavioral Biology* 1, 77-82.
Cain, W.S., & Potts, B.C. (1996). Switch and bait: probing the discriminative basis of odor identification via recognition memory. *Chemical Senses* 21, 35-44.
Cain, W.S., Schiet, F.T., Olsson, M.J., & deWijk, R.A. (1995). Comparison of models of odor interaction. *Chemical Senses* 20, 625-637.
Campbell, B.A., & Sheffield, F.D. (1953). Relation of random activity to food deprivation. *Journal of Comparative and Physiological Psychology* 46, 320-322.
Chang, W.I., Chung, J.W., Kim, Y.K., Chung, S.C., & Kho, H.S. (2006). The relationship between phenylthiocarbimide (PTC) and 6-n-propylthiouracil (PROP) taster status and taste thresholds for sucrose and quinine. *Archives of Oral Biology* 51, 427-432.
Chastrette, M., Thomas-Danguin, T., & Rallert, E. (1998). Modelling the human olfactory stimulus-response function. *Chemical Senses* 23, 181-196.
Conner, M.T., & Booth, D.A. (1988). Preferred sweetness of a lime drink and preference for sweet over non-sweet foods, related to sex and reported age and body weight. *Appetite* 10, 25-35.
Conner, M.T., Booth, D.A., Clifton, V.J., & Griffiths, R.P. (1988a). Individualized optimization of the salt content of white bread for acceptability. *Journal of Food Science* 53, 549-554.
Conner, M.T., Haddon, A.V., & Booth, D.A. (1986). Very rapid, precise measurement of effects of constituent variation on product acceptability: consumer sweetness preferences in a lime drink. *Lebensmittel-Wissenschaft und -Technologie* 19, 486-490.
Conner, M.T., Haddon, A.V., Pickering, E.S., & Booth, D.A. (1988b). Sweet tooth demonstrated: individual differences in preference for both sweet foods and foods highly sweetened. *Journal of Applied Psychology* 73, 275-280.
Conner, M.T., Land, D.G., & Booth, D.A. (1987). Effects of stimulus range on judgments of sweetness intensity in a lime drink. *British Journal of Psychology* 78, 357-364.
Conner, M.T., Pickering, E.S., Birkett, R.J., & Booth, D.A. (1994). Using an individualised attribute tolerance model in consumer acceptability tests. *Food Quality and Preference* 5, 225-232.

Cowart, B.J., & Beauchamp, G.K. (1986). The importance of sensory context in young children's acceptance of salty tastes. *Child Development* 57, 1034-1039.

Crook, C.K., & Lipsitt, L.P. (1976). Neonatal nutritive sucking: effects of taste stimulation upon sucking rhythm and heart rate. *Child Development* 47, 518-522.

Davidson, J.M., Linforth, R.S.T., Hollowood, T.A., & Taylor, A.J. (1999). Effect of sucrose on the perceived flavor intensity of chewing gum. *Journal of Agricultural and Food Chemistry* 47, 4336-4340.

Davis, J.D. (1973). The effectiveness of some sugars in stimulating licking behavior in rat. *Physiology and Behavior* 11, 39-45.

De Graaf, C., Frijters, J.E.R., & Van Trijp, H.C.M. (1987). Taste interaction between glucose and fructose assessed by functional measurement. *Perception and Psychophysics* 41, 383-392.

Denton, D.A. (1982). *Hunger for salt. An anthropological, physiological and medical analysis.* Springer , London, UK.

Derby, C.D., Hutson, M., Livermore, B.A., & Lynn, W.H. (1996). Generalization among related complex odorant mixtures and their components: analysis of olfactory perception in the spiny lobster. *Physiology and Behavior* 60**,** 87–95.

Dessirier, J.-M., Simons, C.T., Iodi Carstens, M., O'Mahony, M., & Carstens, E. (2000). Psychophysical and neurobiological evidence that the oral sensation elicited by carbonated water is of chemogenic origin. *Chemical Senses* 25, 277–284.

Dethier, V.G. (1962). *To know a fly*. New York: McGraw-Hill.

Dibsdall, L.A., Wainwright, C.J., Read, N.W., & Booth, D.A. (1996). How fats and carbohydrates in familiar foods contribute to everyday satiety by their sensory and physiological actions. *British Food Journal* 99, 142-147.

Dibsdall, L. & Booth, D. (1996). Delayed physiological effects of fat and sugar on satiety for food. [SSIB Abstract] *Appetite* 27, 272-273

Ditschun, T.L., & Guinard, J.-L. (2004). Comparison of new and existing methods for the classification of individuals according to 6-n-propylthiouracil (PROP) taster status. *Journal of Sensory Studies* 19, 149-170.

Drewnowski, A., Brunzell, J.F., Sande, K., Iverius, P.H., & Greenwood, M.R.C. (1985). Sweet tooth reconsidered: taste responsiveness in human obesity. *Physiology and Behavior* 35, 617-622.

Drewnowski, A., & Greenwood, M.R.C. (1983). Cream and sugar: human preference for high-fat foods. *Physiology and Behavior* 30, 629-633.

Drewnowski, A., Grinker, J.A., & Hirsch, J. (1982). Obesity and flavour perception: multidimensional scaling of soft drinks. *Appetite* 3, 361-368.

Duclaux, R., Feisthauer, J., & Cabanac, M. (1973). Effect of eating a meal on pleasantness of food and non-food odors in man. *Physiology and Behavior* 10, 1029-1033.

Durlach, P.J., Elliman, N.A., & Rogers, P.J. (2002). Drinking while thirsty can lead to conditioned increases in consumption. *Appetite* 39, 119-125.

Epstein, L.H., & Leddy, J.J. (2006). Food reinforcement. *Appetite* 46, 22-25.

Fechner, G.T. (1860). *Elemente der psychophysik*. Volumes 1 & 2. Leipzig: Breitkopf & Hartel. Translated into English by H.E. Adler in D.H. Howes & E.G. Boring (Eds.) (1966), *Elements of psychophysics*. New York: Holt.

Freeman, R.P.J., Richardson, N.J., Kendal-Reed, M.S., & Booth, D.A. (1993). Bases of a cognitive technology for food quality. *British Food Journal* 95 (9), 37-44.

French, S.A., Jeffery, R.W., & Murray, D. (1999). Is dieting good for you? Prevalence, duration and associated weight and behaviour changes for specific weight loss strategies over four years in US adults. *International Journal of Obesity* 23, 320-327.

Fuke, S., & Konosu, S. (1991). Taste-active components in some foods. A review of Japanese research. *Physiology and Behavior* 49, 863-868. *snow crab*

Garcia, J.. Hankins, W.G., & Rusiniak, K.W. (1974). Behavioral regulation of milieu interne in man and rat. *Science* 185, 824-831. *aversions explain appetite*

Garcia, J., Kimeldorf, D.J., & Koelling, R.A. (1955). Conditioned aversion to saccharin results from exposure to gamma radiation. *Science* 122, 157-158.

Garcia, J., & Koelling, R.A. (1966). Relation of cue to consequence in avoidance learning. *Psychonomic Science* 4, 123-124. (Reprinted in L.D. Houck & L.C. Drickamer, editors, *Foundations of animal behaviour. Classic papers with commentaries*, pages 374-375. Chicago: University of Chicago Press, 1996.)

George, D.N., & Pearce, J.M. (2012). A configural theory of attention and associative learning. *Learning and Behavior* 40, 241-254.

Gibson, E.L., & Booth, D.A. (1986). Acquired protein appetite in rats: dependence on a protein-specific need state. *Experientia* 42, 1003-1004.

Gibson, E.L., & Booth, D.A. (1989). Dependence of carbohydrate-conditioned flavor preference on internal state in rats. *Learning and Motivation* 20, 36-47.

Gibson, E.L., Wainwright, C.J., & Booth, D.A. (1995). Disguised protein in lunch after low-protein breakfast conditions food-flavor preferences dependent on recent lack of protein intake. *Physiology and Behavior* 58, 363-371.

Gietzen, D.W., & Aja, S.M. (2012). The brain's response to an essential amin acid-deficient diet and the circuitous route to a better meal. *Molecular Neurobiology* 46, 332-348.

Grill, H.J., & Norgren, R. (1978). The taste reactivity test. I. Mimetic responses to gustatory stimuli in neurologically normal rats. *Brain Research* 143, 263-279.

Guidetti, M., Conner, M.T., Prestwich, A., & Cavazza, N. (2012). The transmission of attitudes towards food: Twofold specificity of similarities with parents and friends. *British Journal of Health Psychology* 17, 346-361.

Hall, K.D., Sacks, G., Chandramohan, D., Chow, C.C., Wang, Y.C., Gortmaker, S.L., & Swinburn, B.A. (2011). Quantification of the effect of energy imbalance on bodyweight. *Lancet* 378, 826-837.

Harris, G., & Booth, D.A. (1987). Infants' preference for salt in food: its dependence upon recent dietary experience. *Journal of Reproductive and Infant Psychology* 5, 97-104.

Harris, G., Thomas, A., & Booth, D.A. (1991). Development of salt taste preference in infancy. *Developmental Psychology* 26, 534-538.

Hill, A.J., Magson, L.D., & Blundell, J.E. (1984). Hunger and palatability: tracking ratings of subjective experience before, during and after the consumption of preferred and less preferred food. *Appetite* 5, 361-371.

Horne, J., Hayes, J., & Lawless, H.T. (2002). Turbidity as a measure of salivary protein reactions with astringent substances. *Chemical Senses* 27, 653-659.

Hovland, C.I. (1937). The generalization of conditioned responses. I. The sensory generalization of conditioned cues with varying frequencies of tone. *Journal of General Psychology* 17, 125-148.

Hull, C.L. (1947). The problem of primary stimulus generalization. *Psychological Review* 54, 120-134.

Hunt, J.N., & Pathak, J.D. (1960). The osmotic effects of some simple molecules and ions on gastric emptying. *Journal of Physiology* 154, 254-269.
Hunt, J.N., & Stubbs, D.F. (1975). Volume and energy contents of meals as determinants of gastric emptying. *Journal of Physiology* 245, 209-225.
Irvine, M.A., Brunstrom, J.M., Gee, P., & Rogers, P.J. (2013). Increased familiarity with eating a food to fullness underlies increased expected satiety. *Appetite* 61, 13-18.
Iwayama, K., & Eishima, M. (1997). Neonatal sucking behaviour and its development until 14 months. *Early Human Development* 47, 1-9.
Jacobs, H.L. (1958). Studies on sugar preference. 1. The preference for glucose solutions and its modification by injections of insulin. *Journal of Comparative and Physiological Psychology* 51, 304-310.
Jacobs, H.L. (1962). Some physical, metabolic, and sensory components in the appetite for glucose. *American Journal of Physiology* 203, 1043-1054.
Jacobs, H.L., & Sharma, K.N. (1969). Taste versus calories: sensory and metabolic signals in the control of food intake. *Annals of the New York Academy of Sciences* 157, 1084-1112.
Jinks, A., & Laing, D.G. (2001). The analysis of odor mixtures by humans: evidence for a configurational process. *Physiology and Behavior* 72, 51-63. b
Jones, L.V., Peryam, D.R., & Thurstone, L.L. (1955). Development of a scale for measuring soldiers' food preferences. *Food Research* 20, 512-520.
Kay, L.M., & Stopfer, M. (2006). Information processing in the olfactory systems of insects and vertebrates. *Seminars in Cell Development Biology* 17, 433-442.
Kelly, K.A. (1980). Gastric emptying of liquids and solids: roles of proximal and distal stomach. *American Journal of Physiology* 239(2), G71-G76.
Kendal-Reed, M., & Booth, D.A. (1992a). Human odor perception by multidimensional discrimination from remembered patterns. *Chemical Senses* 17(5), 649 (AChemS Abstract 142).
Kendal-Reed, M., & Booth, D.A. (1992b). Olfactory perception as receptor pattern recognition. *Chemical Senses* 17(6), 848-849 (ECRO Abstract 69).
Kerkhof, I., Vansteenwegen, D., Baeyens, F., & Hermans, D. (2009). A picture-flavour paradigm for studying complex conditioning processes in food preference learning. *Appetite* 53, 303-308.
Kissileff, H.R., Booth, D.A., Thornton, J.C., Pi-Sunyer, F.X., Pierson, R.N., & Lee, J. (2008). Human food intake is discriminatively sensitive to gastric signaling. *Appetite* 51, 759.
Knibb, R.C., & Booth, D.A. (2011). Situation-specific cognitive behavioural self-therapy for erroneously suspected allergy or intolerance to a food. A short self-assessment tool. *Appetite* 57, 439-442.
Knibb, R., Booth, D.A., Armstrong, A., Platts, R., Macdonald, A. & Booth, I.W. (1999). Episodic and semantic memory in reports of food intolerance. *Applied Cognitive Psychology* 13, 451-464.
Krieckhaus, E.E., & Wolf, G. (1968). Acquisition of salt by rats. Interaction of innate mechanisms and latent learning. *Journal of Comparative and Physiological Psychology* 65, 197-201.
Kurtz, A.J., Lawless, H.T., & Acree, T.E. (2009). Reference matching of dissimilar binary odour mixtures. *Chemosensory Perception* 2, 186-194.

Laguna Camacho, A., & Booth, D.A. (under review). Step reduction in weight: the missing measure of the change in weight caused by change in a pattern of eating or exercise. Submitted on 15 September 2013.
Laming, D. (1985). Some principles of sensory analysis. *Psychological Review* 92, 462-485. *Visual only*
Laming, D.R.J. (1986). *Sensory analysis.* London: Academic Press.
Laming, D. (1987). The discrimination of smell and taste compared with other senses. *Chemistry and Industry* (January 1987), 12-18.
Laing, D.G., Link, C., Jinks, A.L., & Hutchinson, I. (2002). The limited capacity of humans to identify the components of taste mixtures and taste-odour mixtures. *Perception* 31, 617-635.
Le Berre, E., Béno, N., Chabanet, C., Etiévant, P., & Thomas-Danguin, T. (2008). Just noticeable differences in component concentrations modify the odor quality of a blending mixture. *Chemical Senses* 33, 389-395.
Le Magnen, J., & Tallon, S. (1966). La periodicité spontanée de la prise d'aliments ad libitum du rat blanc. *Journal de Physiologie* 58, 323-349. *variable MSs*
Leshem, M. (2009). The excess salt appetite of humans is not due to sodium loss in adulthood.
Leshem, M., Saadi, A., Alem, N., & Hendi, K. (2008). Enhanced salt appetite, diet and drinking in traditional Bedouin women in the Negev. *Appetite* 50, 71-82.
Levin, B.E., Dunn-Meynell, A.A., & Routh, V.H. (1999). Brain glucose sensing and body energy homeostasis: role in obesity and diabetes. *American Journal of Physiology - Regulatory, Integrative and Comparative Physiology* 276, R1223-R1231.
Li, X., Staszewski, L., Xu, H., Durick, K., Zoller, M., & Adler, E. (2002). Human receptors for sweet and umami taste. *Proceedings of the National Academy of Sciences, U.S.A*. 99, 4692-4696.
Mace, O.J., Lister, N., Morgan, E., Shepherd, E., Affleck, J., Helliwell, P., Bronk, J.R., Kellett, G.L., Meredith, D., Boyd, R., Pieri, M., Bailey, P.D., Pettcrew, R., & Foley, D. (2009). An energy supply network of nutrient absorption coordinated by calcium and T1R taste receptors in rat small intestine. *Journal of Physiology* 587, 195–210.
Malnic, B., Hirono, J., Sato, T., & Buck, L.B. (1999). Combinatorial receptors codes for odors. *Cell* 96, 713-723.
Marshall, K., Laing, D.G., Jinks, A.L., & Hutchinson, I. (2006). The capacity of humans to identify components in complex odor-taste mixtures. *Chemical Senses* 31, 539-545.
Massei, G., & Cowan, D.P. (2002). Strength and persistence of conditioned taste aversion in rats: evaluation of 11 potential compounds. *Applied Animal Behaviour Science* 75, 249-260.
McBride, R.L. (1983). A JND-scale category-scale convergence in taste. *Perception and. Psychophysics* 34, 77-83.
McBride, R.L. (1988). Taste reception of binary sugar mixtures: psychophysical comparison of two models. *Perception and Psychophysics* 44, 167-171.
McBride, R.L. (1993). Integration psychophysics: the use of functional measurement in the study of mixtures. *Chemical Senses* 18, 83-92
McBride, R.L., & Booth, D.A. (1986). Using classical psychophysics to determine ideal flavour intensity. *Journal of Food Technology* 21, 775-780.
McBride, R.L., & Finlay, D.C. (1990). Perceptual integration of tertiary taste mixtures. *Perception and Psychophysics* 48, 326-330.

McCleary, R.A. (1953). Taste and post-ingestion factors in specific-hunger behavior. *Journal of Comparative and Physiological Psychology* 46, 411-421.
Mei, N. (1985). Intestinal chemosensitivity. *Physiological Reviews* 65, 211-237.
Mei, N., & Garnier, L. (1986). Osmosensitive vagal receptors in the small intestine of the cat. *Journal of the Autonomic Nervous System* 16, 159-170.
Meillon, S., Thomas, A., Havermans, R., L. Pénicaud, L., & Brondel, L. (2013). Sensory-specific satiety for a food is unaffected by the ad libitum intake of other foods during a meal. Is SSS subject to dishabituation? *Appetite* 63, 112-118.
Murphy, C., & Withee, J. (1987). Age and biochemical status predict preference for casein hydrolysate *Journals of Gerontology* 42, 73-77.
Pain, J.F., & Booth, D.A. (1968). Toxiphobia to odors. *Psychonomic Science* 10, 363-364.
Pangborn, R.M., & Pecore, S.D. (1982). Taste perception of sodium chloride in relaytion to dietary intake of salt. *American Journal of Clinical Nutrition* 35, 510-520.
Pearce, J.M. (1994). Similarity and discrimination: a selective review and a connectionist model. *Psychological Review* 101, 587-607.
Pearce, J.M. (2002). Evaluation and development of a connectionist theory of configural learning. *Animal Learning and Behavior*, 30, 73–95.
Pecina, S., & Berridge, K.C. (2005). Hedonic hot spot in nucleus accumbens shell: where do mu-opioids cause increased hedonic impact of sweetness? *Journal of Neuroscience* 25, 11777-11786.
Peryam, D.R., & Giradot, N.F. (1952). Advanced taste test method. *Food Engineering* 24(7), 58-61, 194.
Peryam, D.R., & Haynes, J.G. (1957). Prediction of soldiers' food preferences by laboratory methods. *Journal of Applied Psychology* 41, 2-6.
Peryam, D.R., & Pilgrim, F.J. (1957). Hedonic scale method of measuring food preferences. *Food Technology* 11(September), 9-14.
Pfaffmann, C. (1960). The pleasures of sensation. *Psychological Review* 67, 253-268.
Pfaffmann, C. (1964). Taste, its sensory and motivating properties. *American Scientist* 52, 187-206.
Pfaffmann, C., Norgren, R., & Grill, H.J. (1977). Sensory affect and motivation. *Annals of the New York Academy of Sciences* 290, 18-34.
Pfeiffer, J.C., Hort, J., Hollowood, T.A., & Taylor, A.J. (2006). Taste-aroma interactions in a ternary system: a model of fruitiness perception in sucrose/acid solutions. *Perception and Psychophysics* 68, 216-227.
Pliner, P. (1994). Development of measures of food neophobia in children. *Appetite* 23, 147-163.
Polak, E. (1973). Multiple profile – multiple receptor site model for vertebrate olfaction. *Journal of Theoretical Biology* 40, 469-484.
Prescott, J., & Murphy, S. (2009). Inhibition of perceptual and evaluative odour-taste learning by attention to the stimulus elements. *Quarterly Journal of Experimental Psychology* 62, 2133-2140.
Quine, W.V. (1974). *The roots of reference*. Chicago: Open Court.
Raghunathan, R., Naylor, R.W., & Hoyer, W.D. (2006). The unhealthy = tasty intuition and its effects on taste inferences, enjoyment and choice of food products. *Journal of Marketing* 70, 70-184.
Rescorla, R.A. (1973). Evidence for unique stimulus account of configural conditioning. *Journal of Comparative and Physiological Psychology* 85, 331-338.

Richardson, N.J., & Booth, D.A. (1993). Multiple physical patterns in judgments of the creamy texture of milks and creams. *Acta Psychologica* 84, 93-101.

Richardson, N.J., Booth, D.A., & Stanley, N.L. (1993). Effect of homogenization and fat content on oral perception of low and high viscosity model creams. *Journal of Sensory Studies* 8, 133-143.

Riskey, D.R., Parducci, A., & Beauchamp, G.K. (1979). Effects of context in judgments of sweetness and pleasantness. *Perception and Psychophysics* 26, 171-176.

Rolls, B.J., Rolls, E.T., Rowe, E.A., & Sweeney, K. (1981a). Sensory specific satiety in man. *Physiology and Behavior* 27, 137-142.

Rolls, B.J., Rowe, E.A., Rolls, E.T., Kingston, B., Megson, A., & Gunary, R. (1981b) (1979). Variety in a meal enhances food intake in man. *Physiology and Behavior* 26, 215-221.

Roper, S.D. (2007). Signal transduction and information processing in mammalian taste buds. *Pflügers Archiv – European Journal of Physiology* 454, 759-776.

Roper, S.D., & Chaudhari, N. (2009). Processing umami and other tastes in mammalian taste buds. *Annals of the New York Academy of Sciences* 1170, 60-65.

Rozin, E. (1973). *The flavor-principle cookbook.* New York: Hawthorne Books.

Rozin, P. (1986). Sweetness, sensualiyy, sin, safety, and sociualization: some speculations. In J. Dobbing, editor, *Sweetness*, pp. 99-109. London: Springer.

Rozin, P. (1991). Family resemblance in food and other domains. The family paradox and the role of parental congruence. *Appetite* 16, 92-103.

Rutter, M. (Ed.) (2008). *Genetic effects on environmental vulnerability to disease: state of the art and future directions.* Chichester UK: Wiley.

Schifferstein, H.N.J., & Frijters, J.E.R. (1993). Perceptual integration in heterogeneous taste percepts. *Journal of Experimental Psychology – Human Perception and Performance* 19, 661-675.

Schutz, H.G. (1965). A food action scale for measuring food acceptance. *Journal of Food Science* 30, 365-374.

Sclafani, A. (1995). How preferences are learned: laboratory animal models. *Proceedings of the Nutrition Society* 54, 419-427.

Sclafani, A., & Nissenbaum, J.W. (1988). Robust conditioned flavor preference produced by intragastric starch infusions in rats. *American Journal of Physiology* 255, R672–R675.

Shankar, M.U., Levitan, C.A., Prescott, J., & Spence, C. (2009). The influence of color and label information on flavour perception. *Chemosensory Perception 2*, 53–58.

Sheffield, F.D., & Campbell, B.A. (1954). The role of experience in the spontaneous activity of hungry rats. *Journal of Comparative and Physiological Psychology* 47, 97-100.

Shepard, R.N. (1958). Stimulus and response generalization – tests of a model relating generalization to distance in psychological space. *Journal of Experimental Psychology* 55, 509-523.

Shepherd, R., Farleigh, C.A., & Land, D.G. (1984). Effects of stimulus context on preference judgments for salt. *Perception* 13, 739-742.

Shepherd, R. (1988). Sensory influences on salt, sugar and fat intake. *Nutrition Research Reviews* 1, 125-144.

Shuford, E.H. (1959). Palatability and osmotic pressure of glucose and sucrose solutions as determinants of intake. *Journal of Comparative and Physiological Psychology* 52, 150-153.

Simson, P.C., & Booth, D.A. (1973). Olfactory conditioning by association with histidine-free or balanced amino acid loads. *Quarterly Journal of Experimental Psychology* 25, 354-359.

Sinding, C., Thomas-Danguin, T., Chambault, A., Béno, N., Dosne, T., Claire Chabanet, C., Schaal, B., & Coureaud, G. (2013). Rabbit neonates and human adults perceive a blending 6-component odor mixture in a comparable manner. *PLOS One* 8(1) e53534.

Smith, M.H. (1966). Effect of hypertonic preloads on concurrent eating and drinking. *Journal of Comparative and Physiological Psychology* 61**,** 338-341.

Smith, M., & Duffy, M. (1957). Some physiological factors that regulate eating behavior. *Journal of Comparative and Physiological Psychology* 50**,** 601-608.

Spence, C. (2010). The multisensory perception of flavour. *The Psychologist* 23, 7-??.

Stein, L.J., Cowart, B.J., & Beauchamp, G.K. (2012). The development of salty taste acceptance is related to dietary experience in human infants: a prospective study. *American Journal of Clinical Nutrition* 95, 123-129.

Steiner, J. (1977). Facial expressions of the neonate infant indicating the hedonics of food-related chemical stimuli. In J. M. Weiffenbach (Ed.), *Taste and development. The genesis of sweet preference*, pp. 173-189. Bethesda, MD: U.S. Department of Health, Education and Welfare.

Steiner, J.E., Glaser, D., Hawilo, M.E., & Berridge, K.C. (2001). Comparative expression of hedonic impact: affective reactions to taste by human infants and other primates. *Neuroscience and Biobehavioral Reviews* 25, 53-74.

Stevens, S.S. (1957). On the psychophysical law. *Psychological Review* 64, 153–181.

Stevenson, R.J., & Boakes, R.A. (2003). A mnemonic theory of odor perception. *Psychological Review* 110, 340-364. DOI: 10.1037/0033-295X.110.2.340

Stevenson, R.J., Boakes, R.A., & Prescott, J. (1998). Changes in odor sweetness resulting from implicit learning of a simultaneous odor-sweetness association. *Learning and Motivation* 29, 113-132.

Stroud, S., & Booth, D. (1999). Improved questionnaire assessment of PROP foods' bitterness, predictive of aversions and preferences. *Appetite* 32, 293.

Tatzer, E., Schubert, M.T., Timischl, W., & Simbruner, G. (1985). Discrimination of taste and preference for sweet in premature babies. *Early Human Development* 12, 23-30.

Tepper, B.J., Koelliker, Y., Zhao, L., Ullrich, N.V., Lasnzara, C., d'Adamo, P., Ferrara, A., Ulivi, S., Esposito, L., & Gasparini, P. (2008). Variation in the bitter-taste receptor gene TAS2R38, and adiposity in a genetically isolated population in Southern Italy. *Obesity* 16, 2289-2295.

Thompson, D.A., & Campbell, R.G. (1977). Hunger in humans induced by 2-deoxy-D-glucose: glucoprivic control of taste preference and food intake. *Science* 198, 1065-1068.

Thompson, D.A., Moskowitz, H.R., & Campbell, R.G. (1976). Effects of body weight and food intake on pleasantness ratings for a sweet stimulus. *Journal of Applied Physiology* 41, 77-83.

Tomchik, S.M., Berg, S., Kim, J.W., Chaudhari, N., & Roper, S.D. (2007). Breadth of tuning and taste coding in mammalian taste buds. *Journal of Neuroscience* 27, 10840-10848.

Torgerson, W.S. (1958). *Theory and methods of scaling*. New York: John Wiley**.**

Ulrich, D., Hoberg, E., Rapp, A., & Kecke, S. (1997). Analysis of strawberry flavour – discrimination of aroma types by quantification of volatile compounds. *Zetschrift für Lebensmittel-Untersuchung und -Forschung* 205, 218-223.

Valenstein, E.S., Cox, V.C., & Kakolewski, J.W. (1967). Polydipsia elicited by the synergistic action of a saccharin and glucose solution. *Science* 157, 552-554.

van Aken, G.A. (2010). Modelling texture perception by soft epithelial surfaces. *Soft Matter* 6, 826-834.

Verendeev, A., & Riley, A.L. (2012). Conditioned taste aversion and drugs of abuse. History and interpretation. *Neuroscience and Biobehavioral Reviews* 36, 2193-2205.

Villalba, J.J., & Provenza, F.D. (1997). Nutrient-specific preferences by lambs conditioned with intraruminal infusions of starch, casein, and water. *Journal of Animal Science* 77, 378-387.

Vingerhoeds, M.H., Silletti, E., de Groot, J., Schipper, R.G., & van Aken, G.A. (2009). Relating the effect of saliva-induced emulsion flocculation on rheological properties and retention on the tongue surface with sensory perception. *Food Hydrocolloids* 23, 773-785.

Vickers, Z.M. (1984). Crispness vs. crunchiness – a difference in pitch. *Journal of Texture Studies* 15, 157-163.

Wansink, B., Bascoul, G., & Chen, G.T. (2006). The sweet tooth hypothesis: How fruit consumption relates to snack consumption. *Appetite* 47, 107-110.

Weber, E.H. (1843/1996). *De pulsu, resorptione, auditu et tactu* [On the pulse, breathing, hearing and touch] Translated in *E.H. Weber on the tactile senses*, ed. H.E Ross, D.J. Murray, pp. 23-136. Psychology Press, Hove UK.

Wise, P.M., Olsson, M.J., & Cain, W.S. (2000). Quantification of odor quality. *Chemical Senses* 25, 429-443.

Witherley, S.A., & Pangborn, R.M. (1980). Gustatory responses and eating duration of obese and lean adults. *Appetite* 1, 53-63.

Wittgenstein, L. (1953). *Philosophical investigations.* Oxford: Blackwell

Yamaguchi, S. (1967). The synergistic taste effect of monosodium glutamate and disodium 5'-inosinate. *Journal of Food Science* 32, 473-478.

Yeomans, M.R., & Mobini, S. (2006). Hunger alters the expression of acquired hedonic but not sensory qualities of food-paired odors in humans. *Journal of Experimental Psychology – Animal Behavior Processes* 32, 460-466.

Yeomans, M.R., & Symes, T. (1999). Individual differences in the use of pleasantness and palatability ratings. *Appetite* 32, 382-394.

Yeomans, M.R., Jackson, A., Lee, M.D., Nesic, J., & Durlach, P.J. (2000). Expression of flavour preferences conditioned by caffeine is dependent on caffeine deprivation state. *Psychopharmacology* 150, 208-215.

Yeomans, M.R., Mobini, S., Elliman, T.D., Walker, H.C., & Stevenson, R.J. (2006). Hedonic and sensory characteristics of odors conditioned by pairing with tastants in humans. *Journal of Experimental Psychology – Animal Behavior Processes* 32, 215-228.